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LA JOLLA, CALIFORNIA
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By

H. U. SVERDRUP AND W. H. MUNK

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WIND, SEA, AND SWELL: THEORY OF RELATIONS FOR FORECASTING

By

H. U. Sverdrup and W. H. Munk
University of California
Scripps Institution of Oceanography
La Jolla, Calif.

MARCH 1947

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NOTATION

x	Horizontal coordinate.
z	Vertical coordinate, positive upward from undisturbed sea surface.
t	Time.
p	Pressure.
ρ	Density of water (1.025 g/cm^3).
ρ'	Density of air (1.25×10^{-3} g/cm^3).
u	Horizontal component of particle velocity.
w	Vertical component of particle velocity.
u'	Mass transport velocity.
U	Wind velocity at about 8m above sea surface.
C	Velocity of progress of wave (phase velocity).
V''	Group velocity.
V	Velocity of energy flow associated with wave motion.
L	Wave length.
k	$\frac{2\pi}{L}$
T	Wave period.
σ	$\frac{2\pi}{T}$
a	Wave amplitude.
H	Wave height (from crest to trough).
h	Depth of water.
η	Elevation of sea surface relative to undisturbed level.
μ	Viscosity of water (0.018 at 0° C.).
τ	Stress of wind at sea surface.
E_p	Mean potential energy of wave per unit area.
E_k	Mean kinetic energy of wave per unit area.
E	Mean total energy of wave per unit area.

R_N	Mean rate of energy transfer to wave due to normal wind pressure.
R_T	Mean rate of energy transfer to wave due to tangential wind stress.
R_U	Rate at which wind energy is dissipated below level to which wind velocity is referred.
$R\mu$	Mean rate of energy dissipation due to viscosity.
R_H	Mean rate at which energy is used to change wave height.
R_C	Mean rate at which energy is used to change wave velocity.
ϵ	$\frac{R_N+R_T}{R_U}$
F	Length of fetch.
D	Distance of decay.
g	Acceleration of gravity (980 cm/sec ^{2}).
r	Coefficient of energy partition (0.580).
s	Sheltering coefficient (0.013).
β	C/U (Wave age).
δ	H/L (Wave steepness).
γ^2	Resistance coefficient applicable to wind ($\gamma^2=2.6\times10^{-3}$ for wind velocities >5 m. per sec).
α	$\frac{s}{2\gamma^2}$ (2.50).
A	$2\gamma^2\,\rho'/\rho$ (6.35×10^{-5}).

Subscripts:

F refers to value at end of the fetch.

D refers to values at end of distance of decay.

For all numerical computation, c. g. s. units are employed.

ERRATA

Page v—Right hand column; 6th line from bottom:

For “$A\ 2\gamma^2\rho'/\rho(6.35\times10^{-5})$”, read “$A\ 2\gamma^2\rho'/\rho(6.35\times10^{-6})$”

Page 15—Right hand column, 3rd line of equations from top:

For “$\frac{d\varrho}{d\beta}$”, read “$\frac{d\delta}{d\beta}$”

Page 17—Right hand column, 5th line of equations from top:

For “$\frac{d\delta}{d\beta}+2\beta\delta=0$”, read “$\frac{d\delta}{d\beta}+\frac{2\delta}{\beta}=0$”

Page 18—Left hand column, last line of equations:

For “$\frac{\sqrt{\beta}}{1+\alpha(1-\beta)}$”, read “$\frac{\beta\sqrt{\alpha}}{1+\alpha(1-\beta)}$”

Page 29—Left hand column, 30th line from top:

For “2 feet”, read “2 meters”.

Left hand column, 34th line from top:

For “0.9 feet”, read “0.9 meters”

INTRODUCTION

ORDER to forecast sea and swell from veather data it is necessary to know the charac- of the waves produced by a given wind that vs for a known length of time over a known tch of water, the fetch. Prior to 1942 such wledge was based on empirical relationships y of which were inconsistent among them- es. In the fall of 1942 a need for sea and swell casts arose in connection with the planned sion of North Africa. In order to improve basis for forecasting, the authors began their lies at the request of the Oceanographic Divi- of the Directorate of Weather, Army Air ces.

reliminary conclusions were helpful in the can and Mediterranean operations but con- nt results were not achieved until the summer 943. By that time all oceanographic work been transferred to the United States Navy. er contracts with the United States Hydro- hic Office and the Bureau of Ships, the studies ea, swell, and surf were carried on at an lerated pace.

this paper a close combination of theoretical lusion and empirical knowledge is attempted. n a study of the processes by which energy is smitted from wind to waves, certain energy tions are derived which relate wave height and city to wind velocity, duration of wind, and . In order to solve these equations it is ssary to make certain formal assumptions. physical significance of these assumptions are et obscure but the solutions obtained are in e cases in agreement with empirical relation- s and in other cases they remove inconsisten- which have arisen because the relative import- of the different variables had not been clearly gnized.

he present paper is a revision of a report, d Waves and Swell; A Basic Theory for casting, which was submitted to the Hydro- hic Office in September 1943, but which could be released because of wartime restrictions. he revision a few changes in the theory have made, partly because some of the original assumptions were too arbitrary and partly because some new approaches have been stimulated by C.-G. Rossby's recent studies of wave motion.

When the original paper was prepared it was believed that the results would apply to "the larger waves present" but no attempt was made to describe these larger waves more specifically. It is now proposed to introduce a statistical term and to define "the larger waves" as waves having "average height and period of the one-third highest waves." The waves described by these averages are called "significant waves," because experience gained so far indicates that a careful observer who attempts to establish the character of the higher waves will tend to record the significant waves as defined here. The concept of "significant waves" is important because only the significant waves are known empirically, and because for these waves the classical requirement that crests are conserved is not fulfilled. Therefore, the growth and decay of significant waves do not obey the laws that would apply to the waves of the classical theory, but take place according to other laws that will be developed in this paper.

All solutions which relate waves to wind can be represented as relations between nondimensional parameters, but because the empirical data available in 1943 were too incomplete to be shown in this form, nondimensional presentations could not be used for comparison between theory and observations. Through the efforts of agencies partaking in wave research new and more comprehensive material has now made it possible to check the nondimensional relationships against observations.

As a whole, the changes are few considering the intensity with which wave research has been carried out since 1943. The basic numerical relationships between wave height and period as functions of wind velocity, fetch, duration, and distance of decay differ only slightly from those proposed in 1943 and used subsequently with considerable success in sea and swell forecasting during the war.

In 1942 work on sea and swell forecasting had been started independently in Great Britain, and some of the ideas developed there were of value to the authors, although the numerical relationships differed. Subsequently Commander C. T. Suthons, British Admiralty, developed relationships on an empirical basis which, with a few important exceptions, are similar to the ones presented here.

This paper does not deal with the forecasting technique, but a practical manual in forecasting was prepared in September 1943 on the basis of the 1943 report and published by the Hydrographic Office (1944a) in March 1944. The relation between swell and surf is not covered in the present paper nor in the forecasting manual, but studies of the transformation of waves in shallow water at the Woods Hole Oceanographic Institution; the Beach Erosion Board; the Department of Mechanical Engineering, University of California, Berkeley; and the Scripps Institution led to the joint preparation of second manual on the forecasting of breakers and surf, published by the Hydrographic Office (1944b) in Nover
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much to improve the understanding of the p
lems.

THEORY OF SURFACE WAVES

Waves of Infinitely Small Amplitude

Equations required for subsequent develop- nts will be summarized here. Derivations and cussions of these equations are not repeated ce they are readily available (Lamb, 1932, rdrup et al., 1942). In water of constant th the wave velocity can be represented by ans of the equation of classical hydrodynamics:

$$C^2=\frac{gL}{2\pi}\tanh\frac{2\pi}{L}h \tag{1}$$

ere h is the depth to the bottom and L is the ve length.

fining deep water waves and shallow water ves as:

ep water waves:

$$h>\frac{1}{2}L$$

llow water waves: (2)

$$h<\frac{1}{25}L$$

ation (1) becomes with sufficient accuracy for se special cases:

ep water waves:

$$C^2=\frac{gL}{2\pi} \tag{3a}$$

llow water waves:

$$C^2=gh \tag{3b}$$

This paper deals only with deep water waves' which length, period, and velocity are inter- ated as follows:

$$\begin{gathered}C=\frac{L}{T}=\sqrt{\frac{g}{2\pi}L}=\frac{g}{2\pi}T\\ L=\frac{2\pi}{g}C^2=\frac{g}{2\pi}T^2\\ T=\sqrt{\frac{2\pi}{g}L}=\frac{2\pi}{g}C\end{gathered} \tag{4}$$

The water particles move in circles, the radii of ich decrease exponentially with depth according the relation:

Radius of particle orbit

$$=\frac{1}{2}He^{2\pi z/L} \tag{5a}$$

where z is taken positive upwards; consequently the particle velocity is uniform and has the scalar value

Particle velocity

$$=\frac{\pi}{T}He^{2\pi z/L} \tag{5b}$$

The mean energy per unit area of a wave equals (Lamb, 1932, p. 370)

$$E=\frac{1}{2}\rho ga^2 \tag{6}$$

The rate at which this energy is changed by dissipation equals (Lamb, 1932, p. 624)

$$R_\mu=-2\mu k^3a^2C^2 \tag{7}$$

With every wave there is associated a flow of energy in the direction of propagation of the wave. Let V be the velocity at which energy is transmitted. Then $V\times E$, the rate at which energy flows across a vertical plane of unit width, equals

$$VE=\int_{\infty}^{0} pu\,dz$$

where p is pressure and u is the horizontal component of the particle velocity. For deep water waves (Lamb, 1932, p. 383)

$$VE=\frac{1}{2}\rho ga^2C\sin^2 k(x-Ct) \tag{8a}$$

with a mean value

$$VE=\frac{1}{4}\rho ga^2C=\frac{EC}{2} \tag{8b}$$

Equation (8b) can be interpreted to mean that the entire energy is propagated at half the wave velocity or half the energy at full wave velocity. The significance of these interpretations will be discussed later (p. 6).

Waves of Finite Amplitude

Two theories have been developed for deep water waves of finite amplitude: the Stokes theory dealing with irrotational waves, and the Gerstner theory dealing with a specific type of rotational waves. For the Stokes' waves the velocity of progress depends also upon the steepness of the wave, as expressed by the ratio $\delta=H/L$ (Lamb, 1932, p. 420)

$$C^2=\frac{g}{2\pi}L\left[1+\pi^2\delta^2+\frac{5}{4}\pi^4\delta^4+\ .\ .\ .\ .\ .\ .\ .\ .\right] \qquad (9a)$$

For moderate values of δ the wave form is very nearly trochoidal, but for larger values the troughs become wider and flatter, and the crests steeper. According to Mitchell (Lamb, 1932, p. 418), the greatest possible value of δ is equal to 1/7:

$$\delta_{\max}=1/7 \qquad (9b)$$

When this value is reached the wave profile becomes unstable and the wave breaks. The velocity of progress of a wave for which $\delta \doteq 1/7$ is 1.12 times the velocity of a low wave of the same length.

Generally waves in the ocean are much less steep, and equations 1 to 8 are sufficiently accurate for waves of finite height. The latter differ, however, from waves of very small amplitude in one important respect: the particle velocity is not uniform but is at a maximum when the particles are at the highest point in their orbit and moving in the direction of the wave. Upon the completion of each nearly circular motion the particles have advanced a short distance in the direction progress of the wave and have brought abou small transport of mass (figure 1). The aver velocity of this forward motion during one w period, the mass transport velocity, is deno by u'. In deep water, at a depth z (Lamb, 19 p. 419),

$$u'=\pi^2\delta^2Ce^{4\pi z/L} \qquad ($$

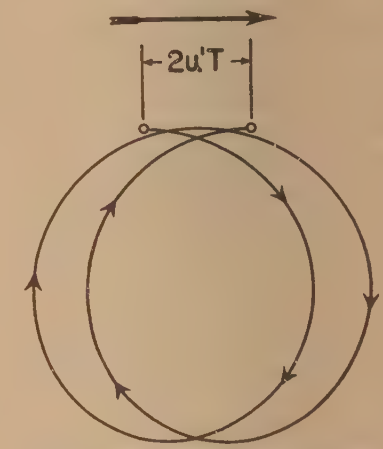


Figure 1.—Orbital motion during two wave periods of a particle in a deep water wave of finite height.

Rossby (1945) has shown the Stokes wave be a special case of an infinite number of poss irrotational waves. His very general treatn has no bearing upon the following discussion the growth of waves, but may modify some of conclusions regarding the propagation of swel

The Gerstner waves are exactly trochoidal equations 1 to 8 are valid for them without proximation. The Gerstner waves are witl mass transport velocity.

PROPAGATION OF A DISTURBANCE THROUGH A REGION PREVIOUS UNDISTURBED

General Considerations and Observations

It has long been a controversial question whether a disturbance of the sea surface in a storm area advances into an area of calm with the velocity of the individual waves, or at half the wave velocity (group velocity). A theoretical investigation, which is presented in this section, leads to the conclusion that for practical purposes the disturbance shall be taken to advance at half the wave velocity. Some waves travel faster and arrive earlier, but their height is probably small.

As a simple form of wave motion, consider a train of waves represented by $\sin k(x—Ct)$ where x is positive in the direction of propagation an is the velocity of transmission of phase, ter wave velocity in this report. If the mediur which the motion occurs is such that C is the s for all wave lengths the velocity C has additi physical significance, it equals V, the rat transmission of energy. If waves are emi from a source in such a manner that full inter is reached with the emission of the very first w any subsequent position of this first wave de a wave front. As an effect of viscosity the he of the wave decreases with increasing dist from the source, but at any given distance

source all waves arrive with the same height
the initial wave. A steady state is reached
n the passage of the wave front.

f, however, the phase velocity C is a function
he wave length, a fact which is expressed by
cribing the medium as dispersive, this ideal
plicity no longer exists. In general, C and V
no longer equal. Radio signals in hollow
les, seismic waves in the interior of the earth,
surface waves in deep water, are examples
vaves traveling through dispersive media. In
se only a portion of the energy travels along
n the wave form, the remaining portion being
behind. Focusing attention on a single wave
leep water, one should expect this wave to
n the portion of the energy left behind by the
ceding one and, in turn, leave a portion of its
rgy for the wave following it. Dealing with a
up of, say, 10 waves, the first wave, which
s energy to the wave behind and gains none
n the front, soon becomes very small, but the
wave, which leaves energy behind, will form
ew wave behind it and become the second from
last.

his is exactly what has been observed and
orted by numerous observers. In the Ad-
alty Navigation Manual (1939), Vol. III, page
, it is stated that:

> otion of the first wave of the group is followed, it will
> ound that this motion dies out and that the wave next
> nd takes the lead. If, on the other hand, the last
> e of the group is watched, another wave will be seen
> ppear behind it. The new waves constantly rise in
> rear as rapidly and as constantly as those in the front
> out, so that the general appearance of a group of waves
> ains unchanged. The group as a whole has a definite
> city of propagation, which has been found to be
> of that of the individual waves comprising the
> up * * *

immel (1911, page 95), also states that:

> * the wave, which at any instant is in front, flat-
> so much as it travels over the surface, that it becomes
> sible after traveling 2–4 meters, whereupon the next
> becomes the first, again goes through the appearance
> attening, etc.

e same experience in tanks is reported in the
hnical Report No. 2 of the Beach Erosion
ard (1942).

> vave tanks, wave groups may be generated by operating
> wave machine through only a few strokes * * *
> observer can follow a particular wave crest only a finite
> ance before it disappears. Close observation reveals
> the wave group maintains its identity, that individual
> es pass through the group, rising out of comparatively
> water at the rear, reaching a maximum at the center,
> then disappearing at the front of the group.

When a long group reaches an observer stationed at a given distance from the source, the initial waves will be very low, but the wave height will increase with time. It will reach a maximum as the center of the group passes the observer and will then decrease. If waves of constant height are continuously generated at the source the observer will find that, after a transient stage of wave growth, a steady state condition involving constant wave height will be approached. The problem is *to find how long it takes to reach, for example, 50 or 90 percent of this constant height.* The problem can also be stated: *to find the rate at which an appreciable portion of the energy of the disturbance is propagated through the area of calm.*

It will be shown that there exists an actual "wave front" which advances with the velocity C of the initial wave but the magnitude of the disturbance so propagated is negligible compared with that of the main group which travels at lower speed.

Group Velocity and Energy Flow

The slow rate at which a disturbance is transmitted through an area of calm, as compared to the rate of travel of the individual waves, is generally explained by stating that the disturbance travels with the group velocity V'. An expression for group velocity is derived by considering the combined effect of two trains of waves of equal wave height whose lengths differ by a small amount dL. The resulting interference pattern will travel with a velocity equal to

$$V'=C-L\frac{dC}{dL}. \tag{11a}$$

Since $C^2 \sim L$, it follows:

$$V'=\frac{C}{2} \tag{11b}$$

(Beach Erosion Board, 1942, p. 32; Cornish, 1934, p. 137; Krümmel, 1911, p. 95.)

This derivation has led to much confusion because, unless further qualified, it would indicate that group velocity is important only under very special conditions as, for example, in the case of two wave trains of equal height and slightly different lengths. But equation (11a) is much more general and can also be derived by making use of methods of summation or integration if the simultaneous existence of an infinite number of wave trains involving a frequency spectrum is assumed (Havelock, 1914, p. 5). If the group velocity V' is defined in such a manner that the wave length L does not vary in the neighborhood of a geometrical point traveling with velocity V',

$$\frac{dL}{dt}=\frac{\partial L}{\partial t}+\frac{\partial L}{\partial x}V'=0 \tag{12}$$

then equation (11a) is valid for any *limited initial disturbance provided the wave crests maintain their identity* (Lamb, 1932, p. 381). This initial disturbance can be expressed in terms of a Fourier integral and the resulting interference pattern derived as a function of time and distance.

As a simple case, assume again that waves of constant height and length are emitted at the source and that their wave length remains constant thereafter. It might appear that under these assumptions only one single wave length is present and that group velocity is not involved. Since, however, the wave train is of finite size the wave length must either equal a constant value L' (within the train), or be zero (outside the train) and this distribution can be represented by a spectrum of wave lengths in a Fourier integral. For long trains the various wave lengths in this spectrum cluster closely about L' but the use of one single wave length is justified only in the case of an infinitely long train.

A study of the propagation of a disturbance into an area of calm could be based on these considerations but we prefer to use a method based on consideration of energy, which appears to be simpler and in better accord with the point of view from which this paper is prepared.

From a comparison of equations (11b) and (8b) follows

$$V'=V$$

This identification of the group velocity with the mean rate of transmission of energy, here shown for deep water waves, can be extended to shallow water waves, indeed to all kinds of waves (Havelock, 1914, p. 55 and p. 61). However, the physical significance does not appear obvious, as evident from explanations attempted by Lamb (1932, p. 383) and Rayleigh (1877, p. 21).

To the present problem it is of particular importance to know whether equation (8b) shall be interpreted to mean that

(1) *all* the energy advances with group velocity, or

(2) *half* the energy advances with wave velocity.

To answer this question consider the flow of energy through a parallelepiped of unit wi
length dx, and extending to a depth below wh
wave motion is negligible (fig. 4, p. 14).
time rate of change of energy within the pa
lelepiped must equal $-\partial(VE)/\partial x$, the net inf
in the direction of the x-axis; and, therefore:

$$\frac{\partial E}{\partial t}+\frac{\partial}{\partial x}(VE)=0$$

In the first case (13) becomes

$$\frac{\partial E}{\partial t}+\frac{C}{2}\frac{\partial E}{\partial x}=0 \qquad (1$$

with the solution

$$E=f\left(x-\frac{C}{2}t\right) \qquad (1$$

which gives no information as to the manne
which E varies with x.

In the second case equation (13) becomes

$$\frac{\partial E}{\partial t}+C\frac{\partial(E/2)}{\partial x}=0$$

leading, as will be shown, to a solution of
transient state which is consistent with neces
physical boundary conditions.

Transmission of Energy by Wave Motio

The difference in form between equations (
and (15) has been given physical significa
equation (15) has been interpreted to mean
the ratio "group velocity to wave veloc
denotes the fraction of energy, E', which adva
with wave velocity.*

$$\frac{E'}{E}=\frac{V}{C}$$

This physical significance follows from a consi
ation of the distribution of potential and ki
energy along a wave. Consider a sinusoidal w
for which the surface elevation is given by

$$\eta=\frac{1}{2}H\sin k(x-Ct)$$

The potential energy is computed from
elevation or depression relative to the still w
surface as:

$$E_P=g\rho\int^{\eta}z\,dz=\frac{1}{8}g\rho H^2\sin^2 k(x-Ct)$$

Substituting in equation (8a) we find for the
at which energy is transmitted

$$VE=CE_P$$

---

*This interpretation is, according to Rossby (1945), not generally val
it is applicable to the type of waves examined here.

icating that the *potential energy is transmitted* *h wave velocity.* The kinetic energy is obtained n the horizontal and vertical components of ticle velocity:

$$E_K=\frac{1}{2}\rho\int_{-h}^{\eta}(u^2+w^2)dz$$

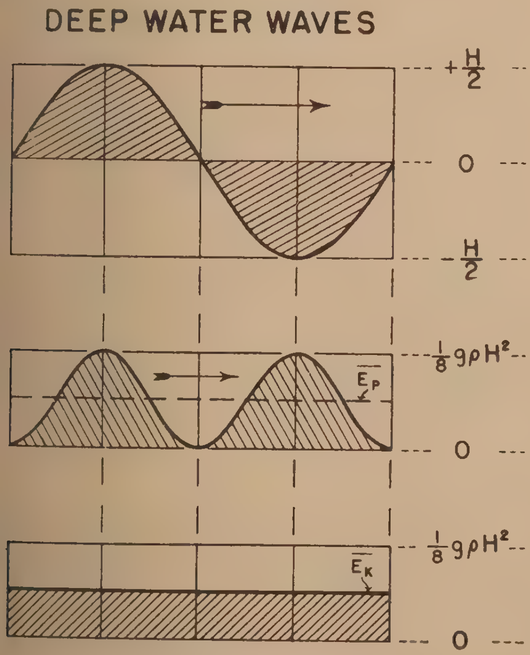
ere h is the depth. For deep water waves,

$$u=\frac{1}{2}H\frac{g}{C}e^{kz}\sin k(x-Ct)$$

$$w=-\frac{1}{2}H\frac{g}{C}e^{kz}\cos k(x-Ct) \text{ and} \tag{19}$$

$$E_K=\frac{1}{16}g\rho H^2 \tag{20}$$

contrast to the potential energy, which is a odic function and advances in phase with the ormation of the surface, the kinetic energy is nly distributed along the entire wave and is ependent of the position or the velocity with ch the surface deformation advances. (See 2.)



e 2.—Variation of surface elevation, potential energy, E_P, and kinetic energy, E_K, along one wave length.

rom (18) we find the mean potential energy a wave length, $\overline{E_P}$,

$$\overline{E_P}=\frac{1}{16}g\rho H^2=E_K=\frac{E}{2} \tag{21}$$

and equation (16) is satisfied, since

$$\frac{E'}{E}=\frac{\overline{E_P}}{E}=\frac{1}{2}=\frac{V}{C}$$

The following interpretation can now be given to observations of wave motion in deep water. Again quoting the Technical Report No. 2 of the Beach Erosion Board (1942):

> As the first wave in the group advances one wave length, its form induces corresponding velocities in the previously undisturbed water and the kinetic energy corresponding to these velocities must be drawn from the energy flowing ahead with the form. If there is equipartition of energy in the wave, half of the potential energy which advanced with the wave must be given over to the kinetic form and the wave loses height. Advancing another wave length another half of the potential energy is used to supply kinetic energy to the undisturbed liquid. The process continues until the first wave is too small to identify. The second, third, and subsequent waves move into water already disturbed and the rate at which they lose height is less than for the first wave. At the rear of the group, the potential energy might be imagined as moving ahead, leaving a flat surface and half of the total energy behind as kinetic energy. But the velocity pattern is such that flow converges toward one section thus developing a crest and diverges from another section forming a trough. Thus the kinetic energy is converted into potential and a wave develops in the rear of the group.

This concept can be interpreted in a quantitative manner, by taking the following example from R. Gatewood (Gaillard 1935, p. 34). Suppose that in a very long trough containing water originally at rest, a plunger at one end is suddenly set into harmonic motion and starts generating waves by periodically imparting an energy $E/2$ to the water. After a time interval of n periods there are n waves present. Let m be the position of a particular wave in this group such that $m=1$ refers to the wave which has just been generated by the plunger, $m=(n+1)/2$ to the center wave, and $m=n$ to the wave furthest advanced. Let the waves travel with constant velocity C, and neglect friction.

After the first complete stroke one wave will be present and its energy is $1/2E$. One period later this wave has advanced one wave length but has left one-half of its energy or $1/4E$ behind. It now occupies a previously undisturbed area to which it has brought energy $1/4E$. In the meantime, a second wave has been generated, occupying the position next to the plunger where $1/4E$ was left behind by the first wave. The energy of this second wave equals $1/4E+1/2E=3/4E$. Repeated applications of this reasoning lead to the results shown in table 1.

The series number n gives the total number of waves present and equals the time in periods since the first wave entered the area of calm; the wave number m gives the position of the wave measured from the plunger and equals the distance from the plunger expressed in wave lengths. In any series, n, the deviation of the energy from the value $E/2$ is symmetrical about the center wave. Relative to the center wave all waves nearer the plunger show an excess of energy and all waves beyond the center wave show a deficit. For any two waves at equal distances from the center wave the excess equals the deficiency. In every series, n, the energy first decreases slowly with increasing distance from the plunger, but in the vicinity of the center wave it decreases rapidly. Thus, there develops an "energy front" which advances with the speed of the central part of the wave system, that is, with half the wave velocity.

Table 1

Distribution of Wave Heights in a Short Train of Waves

Series number n	Wave number, m							Total energy of group
	1	2	3	4	5	6	7	
1	1/2E	------	------	------	------	------	------	1/2E
2	3/4	1/4E	------	------	------	------	------	2/2
3	7/8	4/8	1/8E	------	------	------	------	3/2
4	15/16	11/16	5/16	1/16E	----	------	------	4/2
5	31/32	26/32	16/32	6/32	1/32E	------	------	5/2
6	63/64	57/64	42/64	22/64	7/64	1/64E	--- -	6/2

According to the last line in table 1 a definite pattern develops after a few strokes: the wave closest to the plunger has an energy $E\ (2^n-1)/2^n$ which approaches the full amount E, the center wave has an energy $E/2$, and the wave which has traveled the greatest distance has very little energy $(E/2^n)$.

Approximate Solution to Equation (15)

Let ${}^nR_m={}^nE_mE$, where ${}^nE_m$ denotes the energy of the mth wave in a group of n waves. Then

$$
{}^nR_m=\frac{n!}{2^n}\sum_{r=0}^{r=n-m}\frac{1}{r!(n-r)!} \tag{22}
$$

gives the value of any term in table 1. This table and, therefore, equation (22) are in agreement with observations. It remains to be shown that (22) satisfies the differential equation (15).

$$
\text{Let } t=nT,\ x=mL \tag{23}
$$

where, as usual, T and L denote wave period
length. Then

$$
\frac{\partial R}{\partial n}+\frac{1}{2}\frac{\partial R}{\partial m}=0,\ (R\equiv{}^nR_m)
$$

which can be written as the following differe
equation

$$
\frac{{}^{n+1}R_m-{}^nR_m}{(n+1)-(n)}+\frac{1}{2}\frac{{}^nR_m-{}^nR_{m-1}}{(m)-(m-1)}=0
$$

or

$$
{}^{n+1}R_m-\frac{1}{2}{}^nR_m-\frac{1}{2}{}^nR_{m-1}=0
$$

The general expression for ${}^nR_m$, given by (
satisfies equation (25). The proof, based on
method of mathematical induction, is giver
appendix 1.

Equation (22) is not practicable since we
dealing with such large distances that m ar
have values up to 10^4. The process of summa
would be very cumbersome even if tables o
nominal coefficients were available. From
analogy with the probability theory it is poss
however, to find approximate values of ${}^nR_m$ dire
no matter how large m and n happen to be. S
the binominal coefficnt ${}^nC_r$ is defined as

$$
{}^nC_r=\frac{n!}{r!(n-r)!}
$$

equation (22) can be written

$$
{}^nR_m=\frac{1}{2^n}\sum_{r=0}^{r=n-m}{}^nC_r
$$

The binominal distribution can be cl
approximated by the normal frequency dist
tion curve because the binominal summ
corresponds nearly to the area under the no
curve which is found in tables of the probal
integral. From an analogy with the proba
problem we can write at once

$$
{}^nR_m=\frac{1}{2}-\frac{1}{\sqrt{2\pi}}\int_0^u e^{-\frac{u^2}{2}}du,\quad u=\frac{2m-n-1}{\sqrt{n}}
$$

To find the degree of approximation the app
mate solution (27) is substituted directly i
differential equation (24).

$$
\frac{\partial R}{\partial n}=\frac{\partial R}{\partial u}\frac{du}{dn}=+\left(\frac{1}{\sqrt{2\pi}}e^{-\frac{u^2}{2}}\right)\left(\frac{2m+n-1}{2n^{3/2}}\right.
$$

$$
\frac{1}{2}\frac{\partial R}{\partial m}=\frac{1}{2}\frac{\partial R}{\partial u}\frac{du}{dm}=-\left(\frac{1}{\sqrt{2\pi}}e^{-\frac{u^2}{2}}\right)\left(\frac{1}{\sqrt{n}}\right)
$$

Values of $\frac{\partial R}{\partial n},\frac{1}{2}\frac{\partial R}{\partial m}$, and their differences for n
are given in columns 4–6 of table 2.

'or the center wave (m=450½) the agreement xact, but for all other waves there are found all differences. The approximation is satistory.

Table 2

gree of Approximation Involved in Equation (27)

(1) m	(2) R	(3) $\frac{\vartheta R}{\vartheta u}$	(4) $\frac{\vartheta R}{\vartheta n}$	(5) $\frac{1}{2}\frac{\vartheta R}{\vartheta m}$	(6) $\frac{\vartheta R}{\vartheta n}+\frac{1}{2}\frac{\vartheta R}{\vartheta m}$
300	1.0000	$-.0000$	$+0.00\times10^{-4}$	-0.00×10^{-4}	-0.00×10^{-4}
400	.9996	$-.0014$	$+0.44\times10^{-4}$	-0.47×10^{-4}	-0.03×10^{-4}
420	.9788	$-.0508$	$+16.36\times10^{-4}$	-16.93×10^{-4}	-0.57×10^{-4}
430	.9147	$-.1561$	$+50.84\times10^{-4}$	-52.03×10^{-4}	-1.19×10^{-4}
435	.8485	$-.2347$	$+76.89\times10^{-4}$	-78.23×10^{-4}	-1.34×10^{-4}
440	.7590	$-.3123$	$+102.87\times10^{-4}$	-104.10×10^{-4}	-1.23×10^{-4}
445	.6430	$-.3730$	$+123.57\times10^{-4}$	-124.33×10^{-4}	-0.76×10^{-4}
447	.5920	$-.3882$	$+128.90\times10^{-4}$	-129.40×10^{-4}	-0.50×10^{-4}
449	.5398	$-.3970$	$+132.11\times10^{-4}$	-132.33×10^{-4}	-0.22×10^{-4}
450	.5033	$-.3988$	$+132.86\times10^{-4}$	-132.93×10^{-4}	-0.07×10^{-4}
450½	.5000	$-.3989$	$+132.98\times10^{-4}$	-132.98×10^{-4}	-0.00×10^{-4}
451	.4967	$-.3988$	$+132.86\times10^{-4}$	-132.93×10^{-4}	-0.07×10^{-4}
601	.0000	$-.0000$	$+0.00\times10^{-4}$	-0.00×10^{-4}	-0.00×10^{-4}

Significance of the Solution

'able 2 also illustrates an important point: hin a very short distance the ratio R decreases n very nearly 100 percent to a minute percent. In figure 3, R has been plotted against m, distance in wave lengths from the generating a. The scale to the left gives percent of maxim wave energy, the scale to the right gives cent of maximum wave height; the height io equals the square root of the energy ratio. center wave is halfway between the wave thest advanced and the one at the very rear. energy is exactly one-half the maximum energy, height 70.7 percent of the maximum height. this example the total waves present number , hence the center wave is 450.5 wave lengths from the generating area. Let the "region of sharp decrease in wave height," the shaded portion of the figure, be defined as the region within which the wave heights decrease from 90 to 10 percent of their maximum value. These two limits correspond to m=485, and m=435, and the area of sharp wave decrease is only 50 wave lengths wide.

The "region of sharp decrease in wave height" has at any instant traveled only half as far as the leading wave; its velocity is half the velocity of the leading wave. Therein lies the answer to a controversial question: how fast does a disturbance travel from the storm area, at wave velocity or at half the wave velocity? The answer is that each wave travels with its own wave velocity and arrives at a distance D from the storm area at a time $t'=D/\overline{C}$, where $\overline{C}$ denotes the mean wave velocity. However, these early waves are extremely low. From a practical point of view appreciable waves will appear at D only slightly before $2t'$, the time of arrival of the "center wave." *Hence for purposes of forecasting, the velocity of the disturbance should be taken at one-half the wave velocity.*

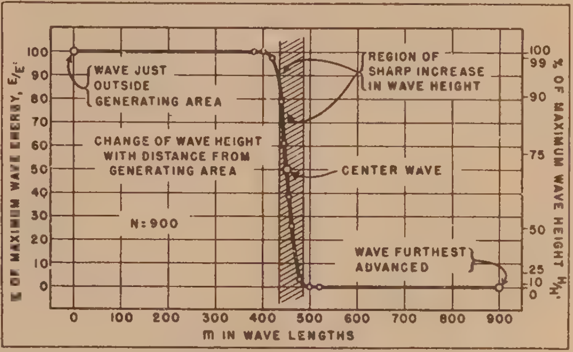


Figure 3.—Change of wave height with distance from source region, assuming that uniform waves produced at the source region advance through water originally at rest. Deep water waves.

ENERGY TRANSFER FROM WIND TO WAVES

Energy Transfer by Normal Pressure

'he average rate at which energy is transferred a wave by normal pressure equals

$$R_N=\frac{1}{L}\int_0^L p_{zz}w_o dx \qquad (28a)$$

ere

$$w_o=-kaC\cos k(x-Ct) \qquad (28b)$$

he vertical component of the particle velocity the surface, and p_{zz} the normal tension acting the sea surface.

When a wind blows, the tension p_{zz}, which is directed opposite to the pressure exerted on the sea surface, can, according to Jeffreys (Jeffreys, 1925 and Lamb, 1932, p. 625), be taken as the sum of two negative terms, one representing the constant atmospheric pressure and the other, the wind pressure against different portions of the wave:

$$p_{zz}=-p-\Delta p$$

The wind pressure can be considered composed of a series of harmonic terms of wave lengths L,

$2L$, $3L$, ... , but of these terms only the one in phase with w_o does a net amount of work. Jeffreys assumes this term to be proportional to the product of the density of the air, the square of the wind velocity, and the slope of the surface:

$$\Delta p=s\rho'(U-C)^2\frac{\partial\eta}{\partial x}=s\rho'(U-C)^2ka\cos k(x-Ct) \tag{29}$$

and he calls the coefficient of proportionality, s, the "sheltering coefficient." It might be more descriptive to use the term "streamlining coefficient" because the coefficient is a measure of the form resistance offered by the wave.

From (28a), (28b), and (29) it follows:

$$R_N=+\frac{1}{2}s\rho'(U-C)^2k^2a^2C \text{ for } C<U \tag{30a}$$

Equation (30a) holds for waves traveling more slowly than the wind. Should the wave velocity exceed that of the wind, and the relative wind velocity be directed against the direction of wave motion, then Δp is 180° out of phase with the slope of the wave, and the sign in equations (29) and (30a) must be reversed. Hence

$$R_N=-\frac{1}{2}s\rho'(U-C)^2k^2a^2C \text{ for } C>U \tag{30b}$$

Jeffreys assumes R_N to be the only important source of wave energy. On this assumption the energy of a wave can increase only if R_N exceeds R_μ, the rate at which energy is dissipated by viscosity, or if, according to (7) and (30), using (3a),

$$s\rho'(U-C)^2C>4\mu g \tag{31a}$$

This is Jeffreys' criterion for the growth of deep water surface waves. According to (31a), waves cannot grow if, approximately,

$$C>U-\sqrt{\frac{4\mu g}{s\rho' U}} \tag{31b}$$

and the wave velocity cannot exceed the wind velocity during the stage of growth. Jeffreys evaluated s from equation (31a) by noting that for a given wind velocity the term on the left-hand side is at a maximum when

$$C=\frac{1}{3}U \tag{32a}$$

The least wind which can maintain waves is, therefore,

$$U_{\min}=3\left(\frac{\mu g}{s\rho'}\right)^{\frac{1}{3}} \tag{32b}$$

Observations by Jeffreys gave $U_{\min}$ appr mately 110 cm/sec. With this value and $\mu=0.018$, $g=980$, and $\rho'=1.25\times10^{-3}$, one obt $s=0.27$.

The corresponding wave velocity is $U_{\min}/3$ about 35 cm/sec, the corresponding wave lengt 8 cm, and the wave period

$$T_{\min}\doteq 0.22 \text{ seconds}$$

Observations by others agree as to the orde magnitude of the least wind velocity and smallest wave length.

The mechanism described by Jeffreys appe therefore, to give a satisfactory explanation the initial formation of waves. *However, not possible to apply Jeffreys' concept and numerical value of s when studying the growt waves after their initial formation because observed increase in wave height indicates tha transfer of wind energy is only about one-tent that demand by Jeffreys.* This conclusion is stantiated by experiments conducted with s wooden models of waves placed in a wind tu (Stanton, 1937). The pressure distribution a the wave profile was measured and the ampli of the component in phase with w_o (28b) d mined from a harmonic analysis of the pres distribution. The sheltering coefficient can evaluated from these measurements, using e tion (29),

$$s=\frac{\Delta pL}{\rho' U^2\pi H}$$

The results are summarized in table 3.

Table 3

Determination of Sheltering Coefficient F Experiments by Sir Thomas Stanton (19

Diameter of wind tunnel (inches)	Wave length (cm)	Wave height (cm)	Wind velocity (cm/sec)	
12	10.8	.055	325	0.
12	10.8	.55	470	
12	21.6	1.1	330	
12	21.6	1.1	580	
36	7.6	0.75	1,400	
Average				

Although the measurements were subje large experimental errors as indicated by the variation in s, the average shows clearly Jeffreys' value of 0.27 is too high.

Energy Transfer by Tangential Stress

ffreys did not take into account a transfer of gy by tangential stress because he considered process as negligible compared to the transfer ormal pressure, but the following considera- s show that tangential stress cannot be ected.

he average rate at which energy is transmitted he wave by tangential stress equals

$$R_T=\frac{1}{L}\int_0^L \tau u_0 dx \qquad (33)$$

re u_0 denotes the horizontal component of icle velocity at the sea surface and where τ is stress which the wind exerts on the sea ace.

t wind velocities above 500 cm/sec the stress he wind equals (Rossby, 1936)

$$\tau=\gamma^2\rho' U^2, \qquad (34a)$$

re ρ' is the density of the air, U is the wind city at a height of 8 to 10 m and γ^2 is the tance coefficient.

arious types of observations have consistently to the value

$$\gamma^2=2.6\times 10^{-3} \qquad (34b)$$

vided that the wave velocity does not differ too h from the wind velocity. If this condition is fulfilled the value of γ^2 is probably greater. roducing (34a) in (33), assuming τ to be in- endent of x:

$$R_T=\gamma^2\rho' U^2 \int_0^L \frac{1}{L}u_0 dx \qquad (35)$$

or waves of small amplitude

$$u_0=\pi\delta C \sin k(x-Ct)$$

the integral in (35) vanishes. This, appar- y, led Jeffreys to assume that energy trans- ted by tangential stress does not play an ortant part in the generation of waves. For kes' waves of finite amplitude, which are ompanied by mass transport (10), the integral 35) has the value

$$u'_0=\pi^2\delta^2 C \qquad (36)$$

, therefore,

$$R_T=\gamma^2\pi^2\rho'\delta^2 C U^2 \text{ (for } U>500 \text{ cm/sec)} \qquad (37)$$

t would be more correct to write $(U-u'_0)^2$ U^2 in equation (37), since stress is caused by wind velocity relative to the water surface, since u'_0 is small compared to U, (37) gives a sfactory approximation.

The energy of waves can increase only if (R_N+R_T) the rate at which energy is added by both normal and tangential stresses of the wind exceeds R_μ, the rate at which energy is dissipated by viscosity, or if, according to (7), (30), and (37),

$$\pm s\rho'(U-C)^2C+2\gamma^2\rho' U^2 C>4\mu g \qquad (38)$$

where + refers to $C<U$.

Equation (38) now takes the place of (31), the Jeffreys criterion for the growth of waves. According to the latter, waves cannot attain velocities exceeding the wind velocity, but equation (38) does not place this restriction upon the development. Take, for example, $C=U$ and let $U=500$ cm/sec, the lowest wind velocity for which (34) and hence (37) are valid. Then $s\rho'(U-C)^2C=0$, $2\gamma^2\rho' U^2C=812$, and $4\mu g=71$; hence, according to (38), waves continue to grow even after their velocities exceed that of the wind, in agreement with observations. Since it must be assumed that the wave velocity increases the longer the waves travel, the ratio $\beta=C/U$ will indicate the state of development of the wave and can appropriately be considered a parameter which describes the age of the wave.

Equation (38) is valid for $U>500$ cm/sec only and therefore cannot be applied to the problem of the first formation of waves, which takes place when U is about 100 cm/sec. At wind velocities less than about 500 cm/sec the sea surface is hydrodynamically smooth (Rossby, 1936) and the relation between the stress and the wind velocity differs from that expressed by (34a). The problem of the initial formation of waves must therefore be approached in a different manner. It deserves further attention but lies outside the scope of this paper which deals with the growth of wind waves at wind velocities above 500 cm/sec.

It is of interest to compare the accuracy of R_T and R_N, as defined by equations (37) and (30). R_T depends mainly upon the accuracy with which u' and γ^2 (17b) are known. The expression for u' has been checked experimentally and found to be in good agreement with theory. The numerical value of the resistance coefficient γ^2 has been arrived at by several different methods but is, as already stated, applicable only to wind velocities exceeding 5 m/sec, for which the sea surface can be considered hydrodynamically rough. Otherwise it is independent of wind velocity. One might estimate roughly that R_T can be obtained from equation (37) with an accuracy of ±25 percent. The accuracy to which R_N can be obtained from (30) depends mainly upon the knowledge of the "sheltering coefficient" s, and upon the extent to which it remains constant. Especially during the early stages of growth, a variation in s might be expected. A detailed theoretical and experimental investigation of energy transfer by normal stress would be highly desirable because the accuracy to which R_N can be evaluated is less than the corresponding accuracy for R_T. Fortunately, the term R_T plays a more important part in the development of waves than R_N (see p. 23).

Friction

The effect of molecular viscosity is small compared to the wind effects. Collecting constants, by putting $A=2\gamma^2\rho'/\rho$ and $\alpha=s/2\gamma^2$, equations (30), (37) and (7) become:

$$R_T=EAgU^{-1}\beta^{-3} \tag{39}$$

$$|R_N|=EAgU^{-1}\beta^{-3}\alpha(1-\beta)^2 \tag{40}$$

$$R\mu=\frac{-4\mu g^2}{\rho}EU^{-4}\beta^{-4} \tag{41}$$

From equations (39), (40), and (41):

$$\frac{R\mu}{R_T\pm R_N}=-\frac{4\mu g}{\rho A[1\pm\alpha(1-\beta)^2]}U^{-3}\beta^{-1}$$

With $\mu=1.8\times10^{-2}$, $g=980$, $\rho=1$, $A=6.5\times10^{-6}$ and $\alpha=2.5$, as will be shown later:

$$\frac{R\mu}{R_T\pm R_N}=-\frac{1.09\times10^7}{1\pm2.5(1-\beta)^2}U^{-3}\beta^{-1}$$

For $U=500$ and $\beta=0.1$ ($C=50$):

$$\frac{R\mu}{R_T+R_N}=-0.29$$

For $U=1{,}000$ and $\beta=0.1$ ($C=100$):

$$\frac{R\mu}{R_T+R_N}=-0.036$$

For all but very small values of β and for mo ate and large values of U, $R\mu$ is small compare R_T+R_N and can be neglected when dealing the growth of waves.

After waves have left the storm area and t through regions of calm, the effect of ordinary cosity is still negligible. An 8 second wave example, would have to travel more than 2 and could complete 10 "equatorial round t before its height would decrease by 63 pe ($1/e=0.37$).

It may be argued that the rapid decay of w could be explained by introducing an eddy cosity, as is done in order to account for the velocities of wind driven currents. When de with wind currents the eddy viscosity has found to be from 1,000 to 100,000 times as lar the ordinary viscosity, but when dealing waves the introduction of an eddy viscosity s undesirable for the following reasons:

1. The decrease of particle velocity depth would be much more rapid than is s by equation (5), which has been verifie observations.
2. The eddy viscosity applicable to wind rents gives much too rapid a decrease of height, and it would be necessary to intro a smaller coefficient applicable only to motion.
3. The observed decrease of wave heigh be explained as the effect of air resis against the advancing wave.

Assuming, therefore, that dissipation place by ordinary viscosity only, the effe friction is neglected.

THEORY FOR THE GROWTH OF WAVES

"Significant" and "Conservative" Waves

In the last sections we have tacitly assumed the existence of infinite trains of waves, but in the oceans we have to deal with trains of finite length. Within the generating area there always exist a large number of such trains of waves of different lengths, traveling with the wind or at small angles with the wind direction. From interference and criss-crossing there results an extremely irregular appearance of the sea surface, but the larger waves can be recognized and the theoretical relation between period, length, and velocity appl these (Krümmel 1911, Sverdrup et al, 1942).

Because of the simultaneous presence of trains the wave characteristics have to be scribed by some statistical terms. For purpose it has been found convenient to intro "the average height and period of the one- highest waves." The waves defined in manner are called "the significant waves,"

definition requires further refinement because
composition of the "one-third highest waves"
ends upon the extent to which the lower waves
e been considered. Experience so far indicates
t a careful observer who attempts to establish
character of the higher waves will record values
ch approximately fit the definition. It is also
nd that the concept of "significant waves" is
ntial for the purpose of forecasting.

he significant waves behave differently com-
ed to the classical waves in a single finite
n. The wave crests in such a train maintain
r identity, that is, the waves are conserva-
, and according to (12):

$$\frac{\partial C}{\partial t}+\frac{C}{2}\frac{\partial C}{\partial x}=0 \qquad (42)$$

teady state ($\partial C/\partial t=0$) cannot exist simul-
eously with an increase of wave velocity (or
od) with distance in fetch; nor can a transient
e exist during which the wave velocity (or
od) increases with the time but remains uniform
r an area ($\partial C/\partial x=0$).

hese conclusions are in contrast with ordinary
erience as to the behavior of the significant
es. When a wind of constant velocity has
vn for a long time over a limited stretch of
er, such as a lake, a steady state is established.
any fixed locality the significant waves do not
nge with time, but on the downwind side of
lake they are higher and longer than on the
ind side. If, on the other hand, a uniform
l blows over a wide ocean, waves grow just
ast in one region as in any other region and the
ificant waves change with time but do not
in a horizontal direction.

he discrepancy between the behavior of signifi-
t waves and individual waves must lie in the
that the crests of significant waves do not
ntain their identity: in the storm area signifi-
t waves are not conservative. The implica-
s of this conclusion are as yet not clear but
possible that the significant waves represent
rference patterns which in a given locality
formed by ever-changing combinations of
e trains. In all events, relationships between
es and wind, fetch, and duration which shall
e with empirical results must be based on a
ly of significant waves. Such a study repre-
s a radical departure from the study of the
servative waves of the classical theory.

Energy Budget of Conservative and of Significant Waves

The transient (or unsteady) state will be discussed first. The total energy per unit crest width of a wave equals EL, where E is the mean energy per unit surface area. The energy added each second by the normal pressure of the wind equals $\pm R_N L$ (30) and that added by the tangential stress equals $R_T L$ (37).

Only half the energy, the potential energy, travels with the wave (18). Kinetic energy is constantly gathered at the forward edge of the wave, and left behind at the rear edge. This feature can be illustrated by considering a parallelepiped of unit width, extending to a depth below which wave motion is negligible, and whose forward and rear edges travel beneath two adjacent crests (fig. 4). At the forward edge of the moving parallelepiped energy is gained at the rate

$$C\frac{E}{2}+L\frac{\partial}{\partial x}\left(C\frac{E}{2}\right)$$

and at the rear edge energy is lost at the rate $CE/2$.

The total energy budget can therefore be written:

$$\frac{d(EL)}{dt}=\left\{R_T\pm R_N+\frac{\partial}{\partial x}\left(C\frac{E}{2}\right)\right\}L \qquad (43)$$

The rate at which the wave length increases and, therefore, at which the parallelepiped "stretches" is determined by the difference in speed between the adjacent wave crests:

$$\frac{dL}{dt}=\frac{\partial C}{\partial x}L \text{ or } \frac{\partial C}{\partial x}=\frac{1}{L}\frac{dL}{dt}$$

Since $C^2=gL/2\pi$, this equation can also be written

$$\frac{\partial C}{\partial x}=\frac{2}{C}\frac{dC}{dt} \qquad (44)$$

and (43) takes the form:

$$\frac{dE}{dt}+\frac{E}{C}\frac{dC}{dt}-\frac{C}{2}\frac{\partial E}{\partial x}=R_T\pm R_N \qquad (45)$$

In this form the above equation applies to a train of conservative waves, but not to significant waves because experience shows that under the stated conditions the energy of the significant waves is independent of x:

$$\frac{\partial E}{\partial x}=0 \qquad (46)$$

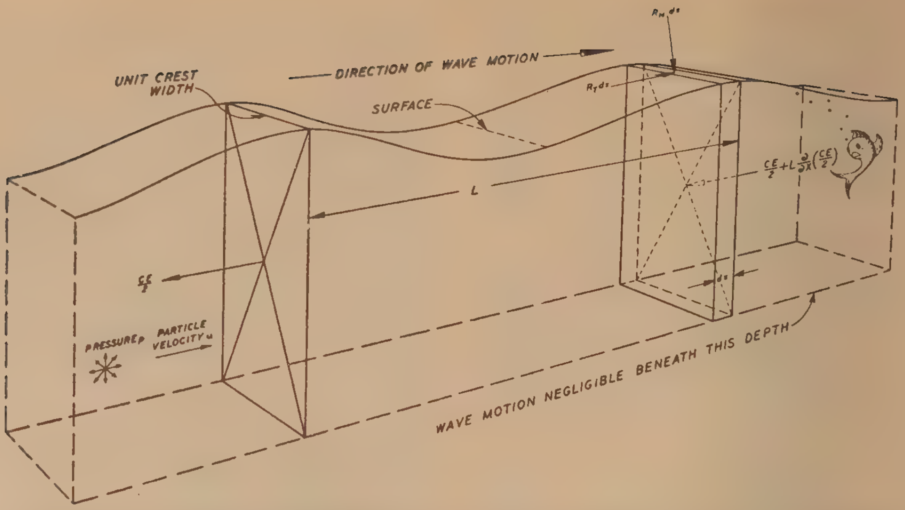


Figure 4.—Energy changes of an individual wave of length L traveling from left to right with velocity C.

With this condition (45) takes the form

$$\frac{dE}{dt}+\frac{E}{C}\frac{dC}{dt}=R_T\pm R_N \qquad (47)$$

which will be further examined. It is not immediately apparent that this equation can be applied to nonconservative systems, but when the constants in the solution are evaluated for the significant waves the results check with observations.

Integration of (47) gives the change with time of the significant waves at any locality in the storm area. Initially the significant waves will have originated in the immediate neighborhood of the locality considered. As the time increases, the waves reaching this locality will have travelled a longer time and originated at larger distances. In practice the distance from which waves can come is limited by the dimensions of the storm system or by a shore line. This distance is called the fetch.

The time necessary for the waves to travel from the beginning of the fetch to the locality in question is called the minimum duration, $t_{\min}$. If the duration of the wind exceeds $t_{\min}$ the character of the significant waves that are present in the fetch remains constant in time: a steady state is established.

To examine the steady state, consider a parallelepiped fixed in space of unit width and length δx, but otherwise similar to the one considered above. Since the parallelepiped is fixed in space, potential energy flows into the volume at the rear edge at the rate $CE/2$ and leaves at the forward edg the rate

$$C\frac{E}{2}+\frac{\partial}{\partial x}\left(C\frac{E}{2}\right)\delta x$$

The local change in energy must equal the su the amounts which enter or leave the paral piped:

$$\frac{\partial E}{\partial t}\delta x=-\frac{\partial}{\partial x}\left(C\frac{E}{2}\right)\delta x+(R_T\pm R_N)\delta x$$

or, rearranging,

$$\frac{\partial E}{\partial t}+\frac{C}{2}\frac{\partial E}{\partial x}+\frac{E}{2}\frac{\partial C}{\partial x}=R_T\pm R_N \qquad ($$

This equation corresponds to (45) and applie conservative waves. In order to apply it tc significant waves which are present over a lin fetch after a steady state has been reached write

$$\frac{\partial E}{\partial t}=0$$

and obtain

$$\frac{C}{2}\frac{dE}{dx}+\frac{E}{2}\frac{dC}{dx}=R_T\pm R_N \qquad ($$

This equation is equivalent to (47) and the ments on the applicability of (47) apply.

The solution of equation (48b) gives the h and velocity as function of fetch after a st state has been reached, that is, for $t\geqq t_{\min}$. I shown later how $t_{\min}$ depends upon fetch and d velocity. The value of $t_{\min}$ determines ther equation (47), the duration equation, or), the fetch equation, is to be used for deter-ing the characteristics of the significant waves. he meaning of equations (47) and (48) can be her illustrated. Let the subscript "x" denote dy state conditions and the subscript "t" sient state conditions. Let

$$R_{Hx}=\frac{C}{2}\frac{dE}{dx} \quad \Big| \quad R_{Ht}=\frac{dE}{dt} \qquad (49a, b)$$

ote the increments of energy going into the ease of wave height, and let

$$R_{Cx}=\frac{E}{2}\frac{dC}{dx} \quad \Big| \quad R_{Ct}=\frac{E}{C}\frac{dC}{dt} \qquad (50a, b)$$

he increments of energy going into the increase vave velocity for the steady and the transient e, respectively. Equations (48) and (47) can be written:

$$+R_{Hx}=R_T\pm R_N \mid R_{Ct}+R_{Ht}=R_T\pm R_N \qquad (51a, b)$$

The Fundamental Equation

ccording to equation (4)

$$H=\delta L=\frac{2\pi}{g}\delta C^2=\frac{2\pi}{g}U^2\delta\beta^2 \qquad (52)$$

ere

$$\delta=\frac{H}{L}\ ,\quad \beta=\frac{C}{U} \qquad (53a, b)$$

are two nondimensional parameters to be called wave steepness and wave age.

According to (6) and (52)

$$\frac{1}{E}\frac{dE}{dx}=\frac{2}{H}\frac{dH}{dx}=\frac{2}{\delta}\frac{d\delta}{dx}+\frac{4}{\beta}\frac{d\beta}{dx} \quad \Big| \quad \frac{1}{E}\frac{dE}{dt}=\frac{2}{\delta}\frac{d}{dt}+\frac{4}{\beta}\frac{d\beta}{dt} \qquad (54a, b)$$

Assuming that δ is a function of β only:

$$\frac{d\delta}{dx}=\frac{d\delta}{d\beta}\frac{d\beta}{dx} \quad \Big| \quad \frac{d\delta}{dt}=\frac{d\delta}{d\beta}\frac{d\beta}{dt}$$

With these substitutions and the expressions for R_T and R_N already given in (39) and (40), the equations for the steady state and the transient state can be written in the form

$$\frac{d\beta}{dx}=2AgU^{-2}\beta^{-3}\frac{1\pm\alpha(1-\beta)^2}{5+2\frac{\beta}{\delta}\frac{d\delta}{d\beta}} \quad \Big| \quad \frac{d\beta}{dt}=AgU^{-1}\beta^{-2}\frac{1\pm\alpha(1-\beta)^2}{5+2\frac{\beta}{\delta}\frac{d\delta}{d\beta}} \qquad (55a, b)$$

where the upper sign (+) refers to $\beta\leqq 1$.

Equations (55) relate the dependent variables δ and β to the independent variables x and t. Complete solutions can be found in one of two ways:

1. Eliminate either δ or β (or the equivalent dimensional terms H, T) from the equations by deriving solutions of the type $\delta=\delta\ (x,t)$ on the basis of completely independent considerations. The study of wave dispersion, for example, does indicate solutions $T=T\ (x,t)$ which, when substituted

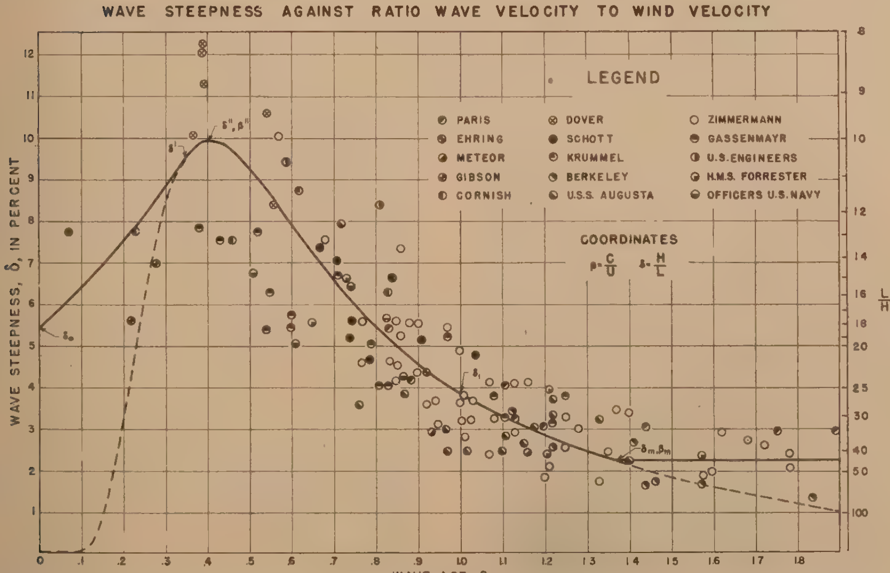


Figure 5.—Relation between wave steepness and wave age. Observed values shown by symbols, assumed relationship shown by full drawn line.

into equations (55) may make it possible to solve for $H=H(x,t)$.

2. Determine a relationship, $\delta=f(\beta)$, between the dependent variables from empirical evidence. The latter procedure has the disadvantage of being semiempirical, but it is the only one found possible so far.

Observations of Wave Age and Wave Steepness

It has been assumed that δ is a function of β only. Such a relationship has already been suggested by Krümmel (1911, p. 82) who writes that "the ratio of wave length to wave height depends upon the stage of development of the waves; in case of a 'young' sea the ratio L/H $(1/\delta)$ equals 10 or may be even smaller, but this ratio increases for a more advanced stage. * * *"

In the past many fruitless attempts have been made to relate wave steepness to wind velocity or other variables, but it has not been attempted to relate steepness, H/L, to wave age, C/U. Such a relationship is suggested by dimensional considerations and, if existing, has the advantage of being independent of fetch and duration. The question can be examined by means of the 128 sets of observations entered in table I of appendix II. The corresponding values of the two nondimensional parameters δ and β are plotted in figure 5, which clearly demonstrates that the two variables are related.

The data have been collected from many different sources and from many localities, varying from a pond at Kensington Park, London, to the trade-wind belt of the North Altantic. Observations listed under Gassenmayr, Officers United States Navy, Paris, and Schott were taken before the turn of the century. Many of these old observations from small vessels are more reliable than recent observations.

Wave data listed under Gibson, Berkeley, and Ehring represent values based upon a statistical analysis of instrumental records. Gibson recorded waves against a pole in Buzzards Bay by means of a moving-picture camera, and the wave characteristics entered in the table apply to the average of the one-third highest of 20 or 30 waves. The Berkeley observations were taken from a United States Navy Weather Patrol ship by means of an automatic pressure-recording instrument and the wave characteristics apply to the one-third highest of a small number of waves. The single point in figure 5, which is based on the observations discussed by Ehring, deserves particular attenti
It gives the significant wave age and steepr
derived from a statistical analysis of 579 wa
from a 30-minute instrumental record in the Nc
Sea. Observations marked U. S. S. *Augusta* w
taken by a weather officer during the invasior
Normandy those marked H. M. S. *Forrester* du
an Atlantic crossing in February 1944. Sc
casual observations at Dover prior to the inva
of the continent are also included. The obse
tions mentioned in this paragraph were obtai
from unpublished reports.

According to figure 5 the steepness reaches a m
imum value of about 0.10 as stated by Krüm
and as has been mentioned in reports from G
Britain. The maximum steepness occurs fo
approximately 0.4, drops off somewhat for you
waves and diminishes rapidly for older waves.

Derivation of an Equation for Wave Age a
Steepness

An empirical curve could be fitted to
empirical data shown in figure 5, and equat
(55) and (54) could be integrated numeric
Instead, an analytical relationship between δ
β will be chosen and the integration will be car
out analytically. The choice of the relation
can be guided by physical considerations.
common experience that the wave period incre
continuously* with x or t. Evidence will be g
later but here it will be assumed that

$$R_C>0$$

If it is assumed that the energy transmitte
the waves by tangential and normal pressur
divided in a certain fixed manner between
energy required to increase wave height (R_H)
wave velocity (R_C), then either of equations
can be split up in the following manner:

$$R_H=(1-r)R_T\pm\left(1+\frac{r}{\alpha}\right)R_N$$

$$R_C=rR_T\mp\frac{r}{\alpha}R_N$$

where the signs are determined by (56).
tion of equations (57a) and (57b) leads to

---

*Leonardo da Vinci was familiar with this when he wrote: "L'onda
piu si muove piu si abassa, e piu si dilata a piu fa veloce" (the further
moves, the more its height decreases and its length and velocity incr

roducing the definitions of R_C, E_T, and R_N into
b) gives

$$\frac{d\beta}{dx}=2AgU^{-2}\beta^{-3}r[1\mp(1-\beta)^2] \tag{58a}$$

$$\frac{d\beta}{dt}=AgU^{-1}\beta^{-2}r[1\mp(1-\beta)^2] \tag{58b}$$

by comparison with (55) leads to the following
lytical relationship between δ and β:

$$\frac{1\pm\alpha(1-\beta)^2}{5+2\dfrac{\beta}{\delta}\dfrac{d\delta}{d\beta}}=r[1\mp(1-\beta)^2] \tag{59}$$

greement between equation (59) and the
pirical data in figure 5 for all but the youngest
ves justifies the assumptions made regarding
"energy split-up." It would have been pos-
e to establish an equation involving δ and β
applying certain technique of curve fitting,
in view of the scatter of the observations it
med preferable to find the relationship from
sical assumptions and to use the observations
evaluate the constants.

quation (59) can be written:

$$\frac{d\ln\delta}{d\beta}=\frac{1+\alpha-2(r+\alpha)\beta+(r+\alpha)\beta^2}{2r\beta^2(2-\beta)}-\frac{2}{\beta}, \quad 0\leqq\beta\leqq1 \tag{60a}$$

$$\frac{d\ln\delta}{d\beta}=\frac{1-r-(r+\alpha)(\beta-1)^2}{2r\beta[1+(\beta-1)^2]}-\frac{2}{\beta}, \quad 1\leqq\beta \tag{60b}$$

ose integrals are

$$\ln\frac{\delta}{\delta_1}=-\frac{1+\alpha}{4r}\,\frac{1-\beta}{\beta}-\frac{1+\alpha}{8r}\ln(2-\beta)+\frac{3\alpha+20r-1}{8r}\ln\frac{1}{\beta}, \quad 0\leqq\beta\leqq1 \tag{61a}$$

$$n\frac{\delta}{\delta_1}=-\frac{\alpha+10r-1}{4r}\ln\beta-\frac{1+\alpha}{8r}\ln[1+(\beta-1)^2]+\frac{1+\alpha}{4r}\tan^{-1}(\beta-1), \quad 1\leqq\beta \tag{61b}$$

ere δ_1 refers to the wave steepness when
1.

ccording to (61a) $\delta\rightarrow0$ for $\beta\rightarrow0$. This is not
agreement with experience because very young
ves are known to have considerable steepness
l even the smallest waves generated by wind
sts have finite velocities and heights (equation
). For that reason it will be assumed that

$$\left.\begin{aligned}\frac{d\ln\delta}{d\beta}&=m \qquad (62)\\ \ln\delta&=\ln\delta_0+m\beta \qquad (63)\end{aligned}\right\}\beta\leqq\beta'$$

where δ_0 and m are constants to be determined by the conditions that δ and $d\delta/d\beta$ must be continuous at $\beta=\beta'$. Since β cannot be zero, the logarithmic curve should not be drawn all the way to the y-axis but the initial development of the wave is so rapid that the exact form of the logarithmic relationship is of very little consequence to the later development of the wave.

Evaluation of Numerical Constants

The logarithmic relationship (62) is assumed applicable from $\beta=0$, $\delta=\delta_0$ to $\beta=\beta'$, $\delta=\delta'$. Assuming continuity in slope at β', equations (60a) and (62) give

$$m=\frac{1+\alpha-2(r+\alpha)\beta'+(r+\alpha)\beta'^2}{2r\beta'^2(2-\beta')}-\frac{2}{\beta'} \tag{64a}$$

while if δ is to be continuous

$$\ln\delta_0=\ln\delta_1-\frac{1+\alpha}{4r}\,\frac{1-\beta'}{\beta'}-\frac{1+\alpha}{8r}\ln(2-\beta')+\frac{3\alpha+20r-1}{8r}\ln\frac{1}{\beta'}-m\beta' \tag{64b}$$

according to (61a) and (63).

The steepness reaches a maximum, to be denoted by δ'', for $\beta=\beta''$, which is found by setting $d\ln\delta/d\beta=0$ in (60a):

$$\beta''=1-\sqrt{\frac{5r-1}{5r+\alpha}} \tag{64c}$$

The corresponding value of δ'' is given by (61a) for $\beta=\beta''$. At $\beta=1$, $\delta=\delta_1$ by definition.

The wave height reaches a maximum, H_m, for $\beta=\beta_m$, where according to (52)

$$\frac{d\delta}{d\beta}+2\beta\delta=0$$

and, from (60b)

$$\beta_m=1+\sqrt{\frac{1-r}{r+\alpha}} \tag{64\textit{d}}$$

The corresponding value of the steepness, δ_m, can be determined from (61b) by substituting $\beta=\beta_m$.

In choosing numerical values for the constants, particular attention was paid to the point δ'', β''. The theoretical maximum value of δ is ⅐ (9b) but according to Krümmel, British reports, and the data in figure 5, δ does not exceed ⅒. The value of β'' must be approximately 0.4 and that of δ_1, 0.04. These considerations are sufficient to determine the chief constants, r, α, and δ_1. The fourth constant, β', was chosen to give δ_0 approximately 0.05, but its value is only of secondary importance.

In this manner the values of the constants can be determined within fairly narrow limits. In choosing the exact values adjustments were made on the basis of other empirical relationships, particularly the ones dealing with the decay of waves, but by far the greatest emphasis has been placed on the relationship between wave steepness and wave age. The curves in figure 5 are based upon the following exact values of the numerical constants:

Symbol	Value	Source	Symbol	Value	Source
r	0. 580		β''	.407	Equation 64c.
α	2. 500		δ''	.0990	Equation 61a.
m	1. 627	Equation 64a.	δ_1	.038	
δ_0	.0537	Equation 64b.	β_m	1..369	Equation 64d.
β'	.350		δ_m	.0219	Equation 61b.
δ'	.095	Equation 61a.			

Wave heights decrease for $\beta>\beta_m$ but younger and shorter waves which must also be present will be most significant. For that reason the section of the curve to the right of β_m is dotted and will be neglected in practical forecasting.

The solid line in figure 5 is assumed to represent the relationship between significant wave steepness and age. Other relationships, such as wave height and velocity as functions of fetch or duration, and the decay of waves, follow directly and can be compared to observational evidence as check of the validity of our assumptions.

Wave Velocity, Wave Height, Fetch, and Duration

The wave velocity will be expressed in nondimensional form by means of the wave age, $\beta=C/U$.

(a): $0\leqq\beta\leqq\beta'$

Substituting (62) in (55):

$$\frac{d\beta}{dx}=2AgU^{-2}\beta^{-3}\frac{1+\alpha(1-\beta)^2}{5+2m\beta} \qquad (65a)$$

$$\frac{d\beta}{dt}=AgU^{-1}\beta^{-2}\frac{1+\alpha(1-\beta)^2}{5+2m\beta} \qquad (65b)$$

with the solutions

$$\frac{gx}{U^2}=\frac{m}{A\alpha}\left\{\frac{\beta^3}{3}+\frac{K_1}{2}\beta^2+K_2\beta+\frac{1}{2}(2K_2-K_1K_3).\right.$$
$$\left.\ln\left(\frac{\beta^2-2\beta+K_3}{K_3}\right)+K_4\tan^{-1}\left[\frac{\sqrt{\alpha}\beta}{1+\alpha(1-\beta)}\right]\right\} \qquad (66a)$$

$$\frac{gt}{U}=\frac{2m}{A\alpha}\left\{\frac{\beta^2}{2}+K_1\beta+\frac{K_2}{2}\ln\left(\frac{\beta^2-2\beta+K_3}{K_3}\right)+\right.$$
$$\left.(K_2-K_1K_3)\sqrt{\alpha}\tan^{-1}\left[\frac{\sqrt{\beta}}{1+\alpha(1-\beta)}\right]\right\} \qquad (66b)$$

where

$$K_1=\frac{5}{2m}+2=3.536$$

$$K_2=\frac{5}{m}+3-\frac{1}{\alpha}=5.673$$

$$K_3=1+\frac{1}{\alpha}=1.400$$

$$K_4=\sqrt{\alpha}(2K_2-K_1K_3-K_2K_3)=-2.446$$

are combinations of known constants.

(b): $\beta'\leqq\beta\leqq1$

using the upper signs of (58):

$$\frac{d\beta}{dx}=2AgrU^{-2}\beta^{-2}(2-\beta)$$

$$\frac{d\beta}{dt}=AgrU^{-1}\beta^{-1}(2-\beta) \qquad (67$$

with the solutions

$$\frac{gx}{U^2}=\frac{2}{Ar}\left[\ln\frac{2}{2-\beta}-\frac{\beta^2}{8}-\frac{\beta}{2}\right]-K_x$$

$$\frac{gt}{U}=\frac{1}{Ar}[(2-\beta)-2\ln(2-\beta)]-K_t \qquad (68$$

where

$$K_x=3.539\times10^2$$

$$K_t=1.705\times10^5 \qquad (69$$

are constants of integration, chosen to make tions (66) and (68) continuous at $\beta=\beta'$.

(c): $1\leqq\beta$.

Using the lower signs of (58):

$$\frac{d\beta}{dx}=2AgrU^{-2}\beta^{-3}[1+(\beta-1)^2]$$

$$\frac{d\beta}{dt}=AgrU^{-1}\beta^{-2}[1+(\beta-1)^2] \qquad (70$$

with the solutions

$$\frac{gx}{U^2}=\frac{1}{2Ar}\left\{\ln[16(\beta^2-2\beta+2)]+\frac{\beta^2}{2}+\right.$$
$$\left.2\beta-2\tan^{-1}(\beta-1)-5\right\}-K_x$$

$$\frac{gt}{U}=\frac{1}{Ar}[\beta+\ln(\beta^2-2\beta+2)]-K_t$$

where K_x and K_t are the constants in equa (69).

A graph of β against the nondimensional parameter gx/U^2 (equations 66a, 68a, 71 shown in figure 6; against the non-dimens duration parameter gt/U (equations 66b, 68b, in figure 7. The continuity of the solu ughout the entire range is apparent, but in ordance with the assumption that the character he sea surface is determined by the highest es present, β remains constant after reaching alue of β_m (64). Comparison with observa-s, which are indicated by points, will be made r.

Vave height will be represented by the non-ensional parameter gH/U^2. According to :

$$\frac{gH}{U^2}=2\pi\delta\beta^2=f\left(\frac{gx}{U^2}\right) \text{ or } f\left(\frac{gt}{U}\right) \qquad (72)$$

ause $\delta=f(\beta)$ (fig. 5) and $\beta=f(gx/U^2)$ (fig. 6) or $f(gt/U)$ (fig. 7). The wave heights are plotted dimensionally in figures 6 and 7. Comparison observations will be made later.

General Case

o far, the growth of wind waves has been mined in two special cases; the growth with h, assuming constant wind of unlimited dura-, and the growth in time, assuming a constant d blowing over an unlimited fetch. Under ial conditions both fetch and duration are ted, and for any given situation the wave ht and age from the fetch graph (fig. 6) will er, in general, from height and age from the ation graph (fig. 7). The smaller of the two es is considered valid for the following ons.

a wind of constant speed has blown for many rs over a small lake the height of the waves ends entirely upon the distance from the up-d shore. If, on the other hand, a wind has vn for just a few hours over a fetch of several isand miles the limitation of the fetch can be o consequence and the wave height must de-d upon the duration only. Therefore, for any n wind velocity the wave height is determined either the fetch (fig. 6) or the duration (fig. 7), ending upon which of the two factors imposes greater limitation to the full development of waves. This can also be stated by saying t for any given fetch there exists a "minimum" ation, $t_{\min}$, for which the fetch and duration phs give the same wave height and age. If duration is less than $t_{\min}$, the waves are de-nined from the duration graph; if the duration greater than $t_{\min}$, the waves are determined n the fetch graph.

he minimum duration can be expressed by ns of the nondimensional parameter $t_{\min}U/x$ which is found by reading off corresponding values of gx/U^2 and gt/U for various values of β from figures 6 and 7, and dividing:

$$\frac{t_{\min}U}{x}=\left(\frac{gt}{U}\middle/\frac{gx}{U^2}\right)_{\beta} \qquad (73)$$

As a numerical example, assume that a 20 m/sec wind blows in an offshore direction. When the wind first starts to blow, $t=0$ and $H=0$ over the entire fetch (fig. 8A). Five hours later, according to the duration graph, the wave height would equal 4 meters as shown by the straight line in figure 8B, but in the immediate vicinity of the coast the waves will be lower, and at the very beginning of the fetch, at $x=0$, the wave height remains zero. The point marked "P" is placed at the distance from the coast at which a steady state has been established. To the left, upwind from point P, the significant wave height depends upon the fetch only. To the right of P the significant wave height is constant at any given time and its value depends only on the duration of the wind.

As the wind continues to blow, the point P travels downwind. For $t=5$ hours P lies 60 km. from the beginning of the fetch (fig. 8B). For $t=24$ hours P lies 500 km. from the beginning of the fetch (fig. 8C), and after 130 hours when P has advanced 4,500 km. the waves have attained the maximum height and the wave height is everywhere determined by the fetch graph alone (fig. 8D). A similar reasoning applies to the wave velocity or the wave age.

Let x and t be fetch and duration for a chosen value of β, and $x+dx$, $t+dt$, correspond to $\beta+d\beta$. Then the rate at which the influence of the limiting fetch advances, that is, the velocity of the point P, equals

$$\frac{dx}{dt}=\frac{d\beta/dt}{d\beta/dx}=\frac{C}{2} \qquad (74)$$

according to equations (55a, b). Hence the region in which the limiting fetch is dominant expands at group velocity. The same conclusion was reached by Commander Suthons (verbal communication).

When developing the theory of the growth of significant waves, the wind velocity in the generating area has been assumed to be constant in time and space. The limited experience gained so far indicates that satisfactory forecasts can be made on this assumption, especially for wind systems separated by well-defined fronts. It might

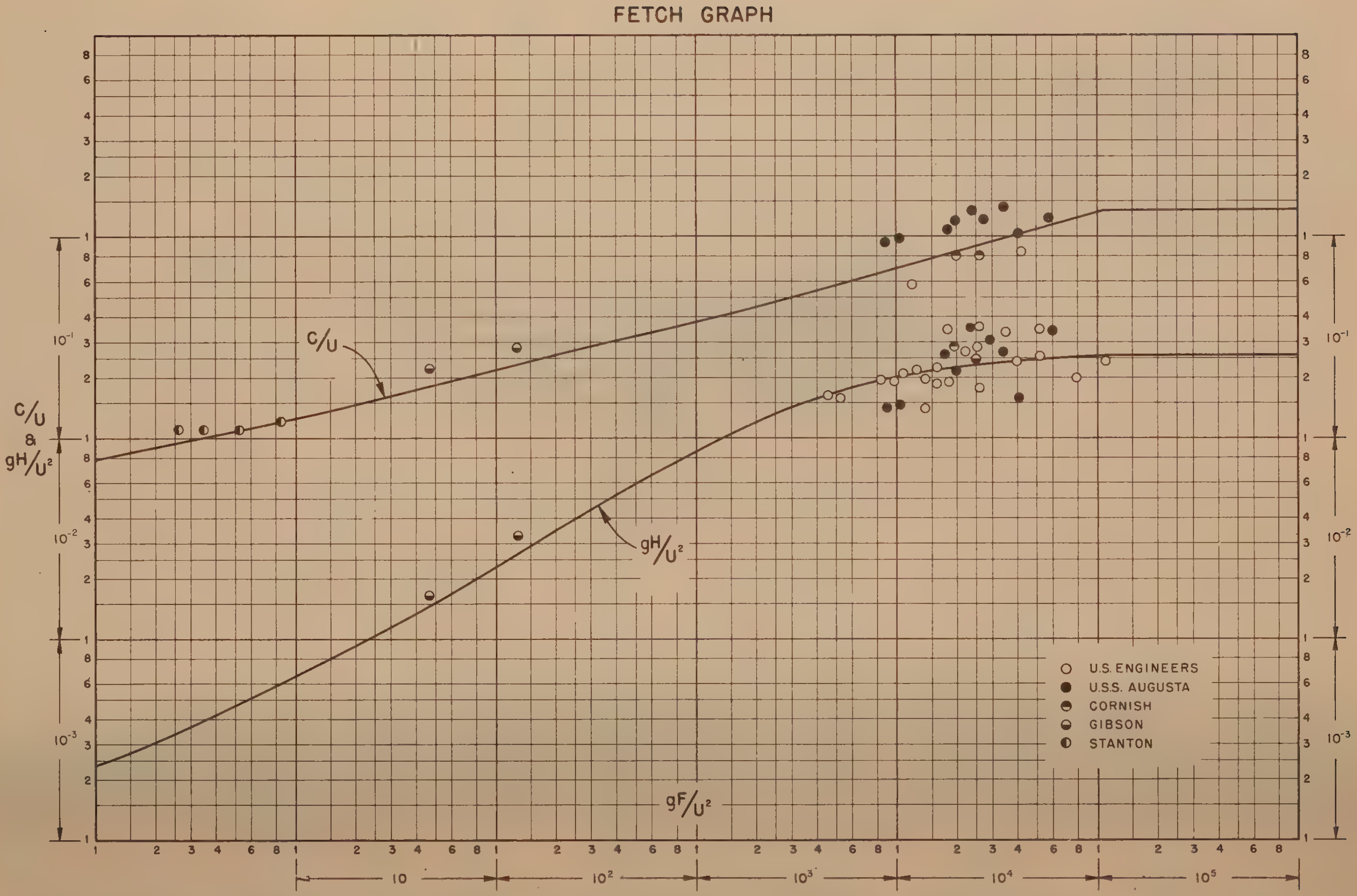
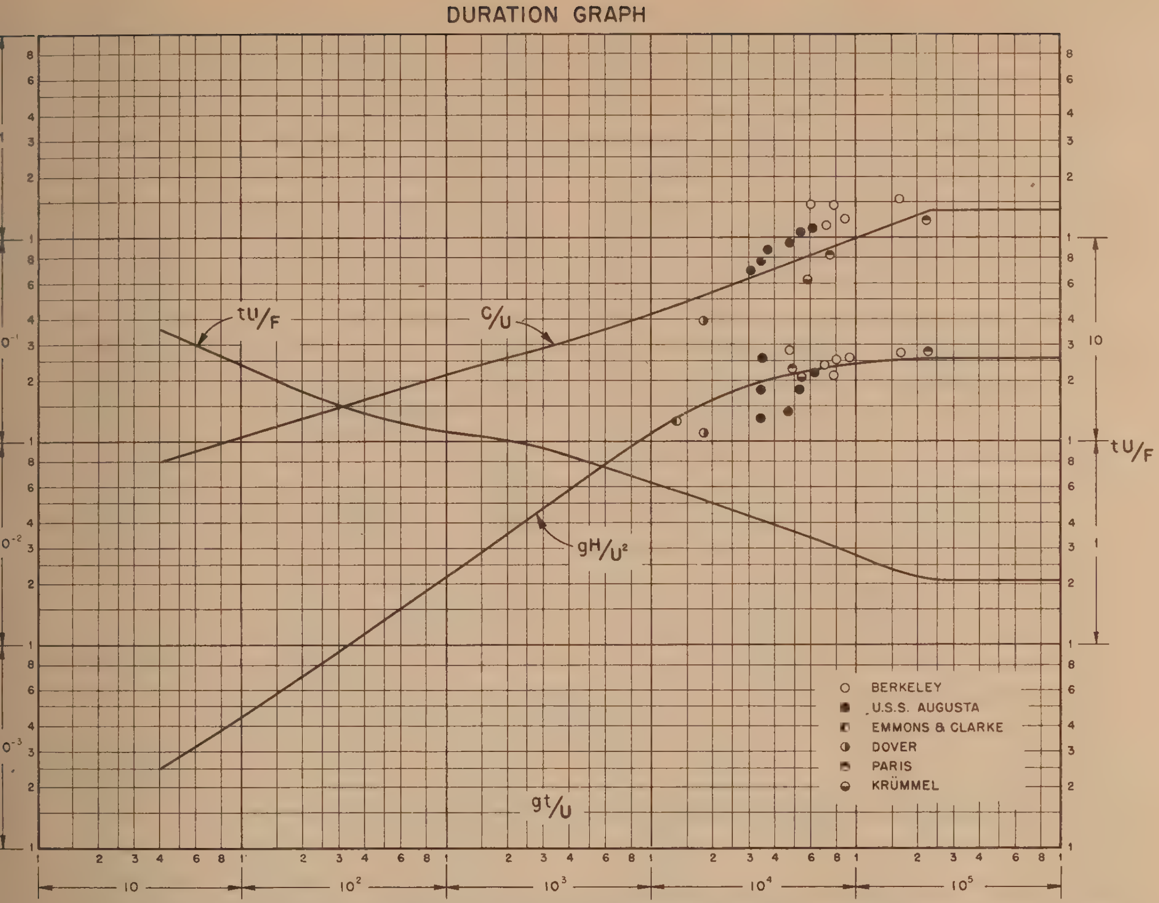


Figure 6.—Wave height and velocity as functions of fetch, using nondimensional parameters. Theoretical relationships shown by curves; observations by symbols.



e 7.—Wave height and velocity as functions of duration, using nondimensional parameters and relation between minimum duration, fetch and wind velocity. Theoretical relationships shown by curves; observations by symbols.

possible to find solutions for the case $U=f(x, t)$ using numerical methods, but such attempts uld involve a great deal of time and labor and uld probably not be justified in view of the ited accuracy with which the fundamental riables, wind velocity, fetch, and duration, can determined.

Wind and Wave Energy

[n the theoretical development dealing with growth of waves solutions to equation (55a, b) re found under two assumptions: the wave riod increases continuously (equation 56), and fundamental equation can be split up into two uations (57a and 57b). The latter assumption ecified the manner in which the contributions of ergy from the two "sources" R_T and R_N, are tributed to the two "energy sinks" R_H and R_C. e energy budget during the generation of waves further illustrated in figure 9 where the light solid curves refer to the energy sources, the dashed curves to the sinks, all expressed as percentage of R_U,

$$R_U=\tau U=\gamma^2\rho' U^3 \qquad (75)$$

the total energy dissipated by the wind in the lowest 8 to 10 meters. The significant wave has an energy income, ϵ', which must equal its total expenditure of energy:

$$\epsilon'=\frac{R_T}{R_U}\pm\frac{R_N}{R_U}=\frac{R_H}{R_U}+\frac{R_C}{R_U} \qquad (76)$$

During the very early stages of wave development most of the energy is transmitted by normal stress, but for β larger than 0.37 transmission by tangential stress is dominant. With a 10 m/sec wind a wave age of 0.37 is reached in 1.88 hours and with a 20 m/sec wind, in 3.75 hours. Therefore, the effect of the normal stresses dominates for a short time only, and during the greater part of the time during which waves grow the effect

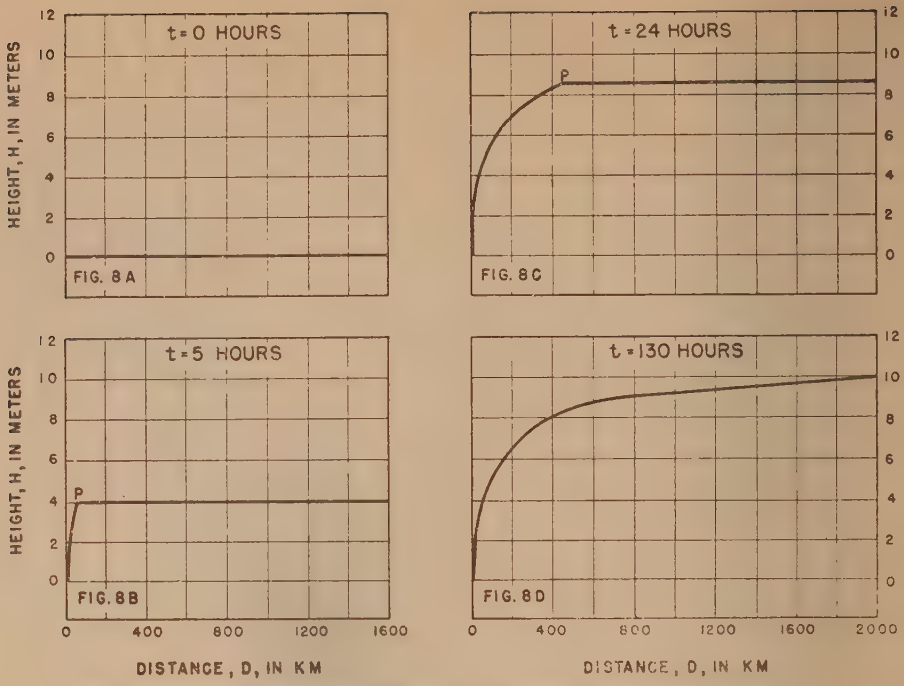


Figure 8.—Growth of wave height with time and distance from beginning of fetch.

of the tangential stress is more important. The ratio between the total amounts of energy transferred by tangential and normal stresses depends upon β only:

β value	0. 37	0. 7	1. 0	1. 369
Ratio between total amounts of energy transferred by tangential and normal stresses	. 87	1. 54	2. 84	4. 43

For $\beta < 1$ the larger portion of the energy goes toward increasing the wave height, for $\beta = 1$ the energy consumed in the increase of wave height and wave velocity are nearly equal, but for very old waves the larger portion of energy is required for the increase of wave velocity.

Again it must be emphasized that as yet no physical significance can be attached to the split-up of the fundamental energy equation. This split-up leads, in what appears to be the simplest mathematical manner, to solutions consistent with empirical evidence, and therein lies its chief justification. Solutions to (55) can perhaps be based on other considerations such as the increase of wave period, but the results obtained here are in such good agreement with observations that the main features in figure 9 can be regarded as significant. Any other attempts to find solut must lead to similar results.

A very small portion, about 1 percent, of wind energy dissipated in the lowest laye transferred to the sea for maintaining the wind current. Another fraction goes into fo tion and maintenance of the significant wa For any given value of β this fraction eq [(76), (39), and (40)]:

$$\epsilon' = \pi^2 \delta^2 \beta^2 [1 \pm \alpha (1-\beta)^2]$$

where

$$\alpha = \frac{s}{2\gamma^2} = 2.5$$

Actually, a number of waves of different ve ties and directions are present simultaneousl that the total percentage, ϵ, of the wind en going into the formation of waves may be tw three times the energy needed for the forma of the significant waves, that is, 10 to 15 per of the wind energy dissipated in the lowest l may go toward increasing and maintaining energy of waves.

With $\alpha = 2.50$ and $\gamma^2 = 2.6 \times 10^{-3}$, one obtains

$$s = 0.013$$

value is lower than that derived from Sir nas Stanton's experiments (table 3), and it is much lower than Jeffrey's value of 0.27. If atter value were valid, it would imply that all the dissipated energy would be required for raising the significant waves alone, but no support can be found for such a contention.

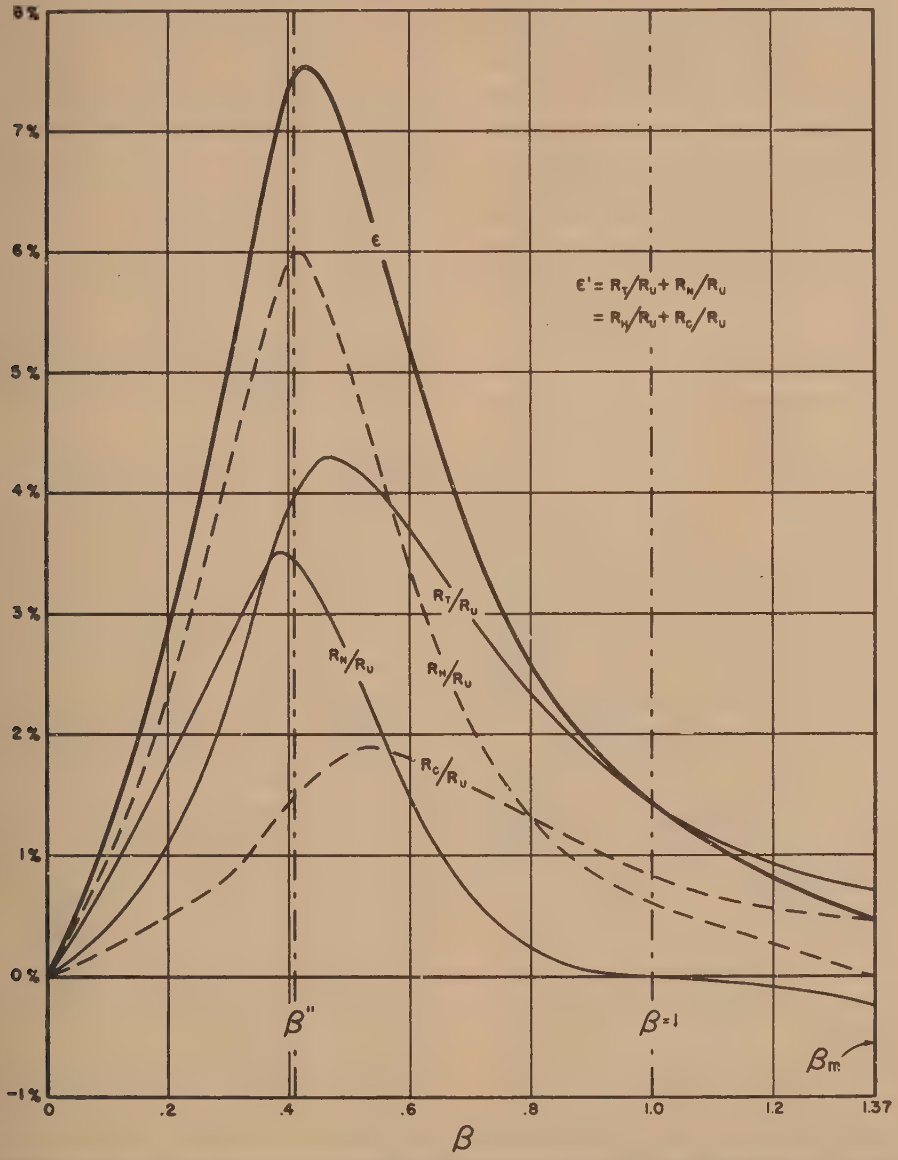


Figure 9.—Energy budget for growing waves. Solid lines show amounts of energy transmitted by normal and tangential wind stresses; dashed lines show amounts needed for changing wave height and wave velocity. All amounts are expressed as percentages of the energy dissipated in the lowest layer of the atmosphere and are shown as functions of wave age.

OBSERVATIONS OF THE GROWTH OF WAVES

he sea surface does not appear as a sequence hythmic waves but in spite of its irregular earance it is possible to apply the terms wave od, wave length, and wave velocity, because e of the waves are more conspicuous than others and their characteristics can be observed. Simultaneous measurements of two or three of the wave characteristics, *C*, *L*, and *T*, afford checks on the possibility of applying the wave theory since they are so interrelated that if one is measured the other two can be computed (equation 4). Numerous measurements (Krümmel, 1911, or Sverdrup et al., 1942, p. 526) are in fair agreement with theoretical expectation. The theory also requires the ratio H/L not to exceed 1/7, a fact fully confirmed by measurements which rarely give values as high as 1/10. Therefore, observations show that the wave formulae are applicable to wind waves.

The empirical knowledge of the relation between wind and waves, however, presents a picture of confusion because the variables which influence the development of waves have not been properly recognized and separated. A complete observation should consist of at least the following five variables:

a. Significant wave height, H.

b. Significant wave period, T, or velocity, C, or length, L.

c. Wind velocity, U.

d. Wind fetch, x.

e. Wind duration, t.

It must furthermore be borne in mind that the waves in any one region are the result not only of local winds but also of winds in other areas, and that the relation between wind and waves during the periods of growth or of decay (sea or swell) should be considered separately.

Although numerous wave observations have been taken, only relatively few are complete in the above sense. Even these observations are unreliable, partly because the measured quantities are poorly defined. For ready comparison with theory, observations of growing waves have been grouped into the following five classes:

	Tabulation	*Graph*
1. δ as function of β	Appendix 2, table I.	Fig. 5.
2a. gH/U^2 as function of gx/U.	Appendix 2, table II.	Fig. 6.
2b. β as function of gx/U	Appendix 2, table II.	Fig. 6.
3a. gH/U^2 as function of gt/U.	Appendix 2, table III.	Fig. 7.
3b. β as function of gt/U	Appendix 2, table III.	Fig. 7.

These dimensionally correct relations will be discussed first, to be followed by a consideration of certain well-known empirical relationships:

4. $H=f(x)$ Stevenson's law.
5. $H=f(t)$ Boergens law.
6. $H=f(U)$ Zimmerman, Cornish, Rossby, and Montgomery, miscellaneous data.
7. $C=f(U)$ Zimmerman, Cornish, Schott, miscellaneous data.

These latter relationships are incomplete.
venson's law, for example, is applicable to "m
mum wind velocities" only, and objections ca
raised to most of the other relationships. It
be shown, however, that the established empi
laws, although dimensionally erroneous,
numerical values which appear reasonable in
light of their nondimensional relations listed ab

1. *Wave age and steepness.*—This relationsh
based on 128 sets of observations, tabulate
table I, appendix 2. The individual observa
have been numbered because they also appe
the other tables where they can be recognize
their number. The observations are plotte
figure 5, where the solid curve is assumed to r
sent the true relationship. Various const
have already been determined on the basis of
curve, and the observations have been previo
discussed (p. 16).

2a. *Wave height against fetch and wind veloci*
The observational material consists of 39 obse
tions from various sources. Those marked
S. ENGINEERS" were taken from the Mil
kee lightship in Lake Michigan (U. S. Engin
1932). The wave height was determined
measuring the rise and fall of the water su
along a graduated line. According to the ori
report, "sufficient readings were taken at
observation for a representative wave height
obtained." Wind velocity, fetch, and dur
were determined from Daily Synoptic S
Northern Hemisphere Sea Level Weather M
but the direct wind observations on the ligh
were also taken into consideration. Accordi
the minimum duration graph in figure 7
observations were limited by fetch.

Observations marked "U. S. S. *Augusta*"
taken visually by Commander R. C. Steere,
off the Normandy Beach Head (unpublishe
ports), and the fetch, duration, and wind vel
were determined from available weather
Cornish (1934) has compiled some of his own
careful observations. Gibson's observations
already been discussed when dealing with
age and steepness (p. 16).

All observations are expressed by the nondi
sional parameters gH/U^2, gx/U and plotte
figure 6. They show good agreement with th

2b. *Wave velocity against fetch and win*
locity.—This relationship can be tested by m
of 19 observations. The wave velocity is
pressed in nondimensional form by the ratio
the wave age. Four observations were obt

tanton (1937) in an experimental 50-foot tank
er closely controlled conditions. The other
ces of observations have been discussed
idy. All observations have been tabulated
le II, appendix 2) and plotted on figure 6,
they are in fair agreement with theory. For
e values of gx/U^2 the observed values lie
tly above the theoretical values. When
nining the agreement between theory and
rvation (fig. 6) it should be considered that
rved values of fetch vary between 50 feet and
e than a thousand kilometers, and that other
meters also vary over wide limits.

. *Wave height against duration and wind
ity.*—Seventeen observations could be found
est this relationship. Observations marked
RKELEY" were taken by means of instru-
ts from weather ships in the Pacific (unpub-
d reports). Fetch, duration, and wind veloc-
vere determined from weather maps. Dura-
s were corrected for initial wave heights
rding to the method given in H. O. Misc.
5. One observation off the coast of Massa-
etts by Emmons and Clarke (unpublished
rt) was adjusted in a similar manner, but the
e height was determined by a photographic
nod. For the latter observation the duration
was unusually well defined since the waves
generated by a storm which formed very
enly. One observation marked "DOVER,"
and, was also taken during a period when the
l rose abruptly from zero to Beaufort 4. Ac-
ing to Krümmel (1911, p. 75), an old observa-
by Paris is of particular interest: "He noticed
es in the southern Indian Ocean rising to an
-all height of 6 to 7 meters as a result of a
ng storm which lasted 4 days or, roughly, 100
s, with remarkable uniformity. The fetch
undoubtedly be set at infinite* * *." This
e height was considered by Krümmel to repre-
the maximum wave height for the existing
l of 16 m/sec, a conclusion which, according to
e 7, agrees remarkably well with theory. The
r observation was taken during the same se-
ice after a duration of only 24 hours. One
rvation by Krümmel himself in the equatorial
fic is also included (Krümmel, 1911, p. 17).
observations available at this time confirm
theoretical relationship between wave height,
$J,^2$ and duration, gt/U, but further observa-
s, particularly for short durations and at very
wind velocities, are very desirable.

3b. *Wave velocity against duration and wind velocity.*—The manner in which all 15 observations plotted in figure 7 were taken has already been discussed. Here the agreement between theory and observations is poorer than it has been for all other relationships. All observations by Berkeley and U. S. S. *Augusta* give high values for the wave velocity; those marked "Dover, Krümmel, and Paris" are too low. Further observations are particularly desirable to check the relationship between wave velocity and duration.

4. *Wave height against fetch.*—Stevenson has established an empirical formula giving the "greatest" wave height, H, in cm. as function of the fetch, x, in cm. (Krümmel, 1911, p. 68), according to which

$$H=0.105\sqrt{x} \qquad (80)$$

The formula was established by means of data from lakes where the value of x ranged from a few kilometers up to about 250 km. Stevenson pointed out that for small values of x the wave heights were greater than those given by the above simple equation. For the Mediterranean, Cornish (1934 p. 33) has verified the relation for fetches up to 830 km., and it is generally assumed that the relationship holds for values of x up to 1,000 km.

The formula is incomplete since it does not take the wind velocity into account but it is intended to apply at the highest wind velocity that can be expected to occur. A few of the observations which served as basis for Stevenson's law did include wind velocity and those, at least, were made during unusually strong winds.

The dimensionless relationship between H, x, and U shown in figure 6 can be made to agree with equation 80 if the following relation existed between fetch and wind velocity:

Fetch (km.)	10	50	100	250	500	1,000
Wind velocity (cm./sec.)	1,230	1,260	1,370	1,600	1,870	2,100

Such a relationship may exist because the wind velocities are higher over water than over land and the greater the body of water, the greater is the "maximum wind velocity" over the water.

5. *Wave height and wind duration.*—According to common experience at sea a high wind can generate a rough sea in a few hours. C. Boergen pointed out (Krümmel, 1911, p. 73) that the height of waves does not increase linearly with the duration of the wind, but that the increase is rapid in the beginning and becomes slower later on. For that reason Boergen suggested a relationship

between wave height and duration of the form

$$H=\frac{H_m}{1+\nu/t} \qquad (81)$$

where H_m is the maximum wave height for any given wind velocity, and ν a coefficient which must be determined from observations. Although a close comparison with the relations given in this report is not possible, the chief features of (81) are in agreement with the present theory.

6. *Wave height and wind velocity.*—According to equation (72) the wave height equals

$$H=\frac{2\pi}{g}U^2\delta\beta^2$$

and depends, therefore, not only upon wind velocity but also upon fetch and duration, since δ and β are functions of these variables. The maximum wave height is found by setting $\beta=\beta_m$, $\delta=\delta_m$ (p. 18) and therefore depends upon the wind velocity only:

$$H_m=\frac{0.26}{g}U^2 \qquad (82)$$

Equation (82) is a dimensionally correct expression and is in fair agreement with the equation

$$H_m=\frac{0.3}{g}U^2 \qquad (83)$$

proposed by Rossby and Montgomery (1935) from entirely different considerations.

Linear relations between wind velocity and the general (not the maximum) wave height have been proposed by Cornish (1934) and Zimmerman (Patton and Marmer, 1932). These relations, together with equation (82) (marked "∞") and (83), are shown in figure 10. Several lines of equal fetch and equal duration have been computed according to the nondimensional relations of this paper and are also shown in figure 10. The points represent the 128 observations of table I, appendix 2, which were plotted on figure 5. Where observations were too crowded for individual plotting they have been combined and are shown by large circles with the number of observations indicated in the center.

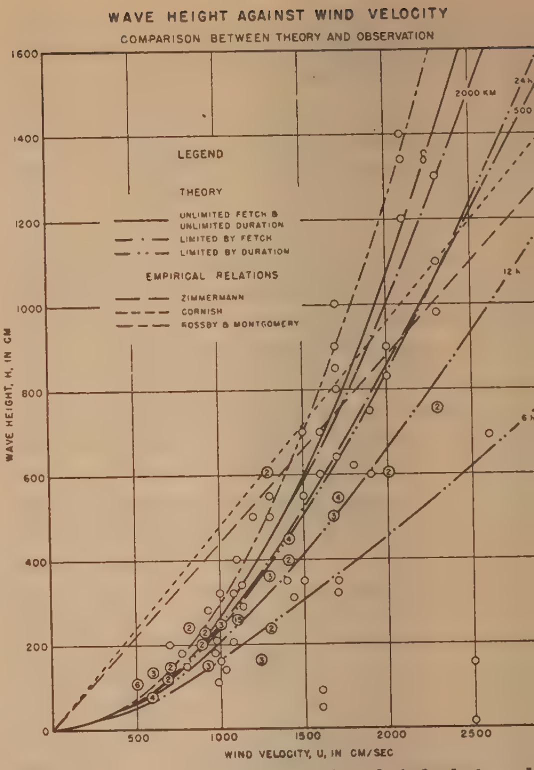


Figure 10.—Wave height as function of wind velocity onl

Equation (82) gives a fair indication of the maximum wave heights but the two linear relationships, which relate wave height to wind velocity only, do not fit well. Some measure of success of these linear relationships may be explained by the fact that the authors have been concerned mainly with the highest waves observed at different wind velocities. These wave hei will be too high at low wind velocities when likely that waves are present which were previc generated by stronger winds or which come f nearby areas. On the other hand, obse wave heights will be too low at very high velocities, where the limitations imposed by fetch and the duration may not have permitt full development of the wave.

7. *Wave velocity and wind velocity.*—Thi lationship is shown in figure 11, the legend of w corresponds closely to that of figure 10. The marked infinity follows from the definitio $\beta_m=C_m/U$ (p. 17). The same 128 sets of obs tions have again been entered. Three emp laws, shown by the thin dashed curves, give empirical relationship between velocity of largest waves and the wind velocity. Accordi Zimmermann (Patton and Marmer, 1932), 2.35 $U^{2/3}$, and hence C exceeds U for wind ve ties above 1331 cm/sec, but according to Co (1934), $C=0.8\ U$, and to Schott (1893), 0.76 U, that is, the wave velocity is less tha wind velocity. Observations in figure 8, how show that the wave velocity frequently ex that of the wind.

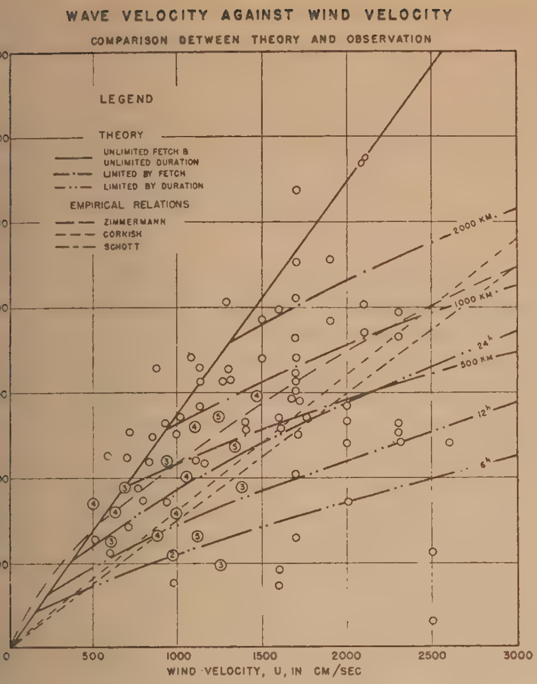


Figure 11.—Wave velocity as function of wind velocity only.

Cornish has discussed the relation between wind d wave velocity in great detail, and his conclu- ns are based on a lifetime of careful observations at sea. It is possible that his conclusions were somewhat influenced by Jeffreys, according to whom waves can grow only if their velocity is less than that of the wind (31), but this limitation no longer holds when the transmission of energy by tangential stress is taken into account (41).

Observations from the trade-wind regions where the wind blows with nearly uniform and moderate velocity over large areas are highly instructive. Some of these observations, which have been plotted in figure 5, are collected in table 4. They were obtained by Paris (Krümmel, 1911, p. 52, 80) and Schumacher (1939) and show clearly that the wave velocities may exceed wind velocities in the generating area.

Table 4
Average Wave Characteristics in Trade Wind Regions

Number table I, appendix 2	Locality	Observations made by—	U cm/sec	C cm/sec	β C/U	δ H/L
32	Trade winds, North Atlantic	Meteor	935	858	0.93	0.029
17	do	do	670	780	1.16	.024
33	do	Paris	590	1,120	1.90	.029
34	Trade winds, Indian Ocean	do	720	1,260	1.75	.029
39	Western Pacific Ocean	do	860	1,240	1.44	.030
47	Westerlies, South Atlantic	do	1,240	1,400	1.13	.032
75	Westerlies, Indian Ocean	do	1,490	1,500	1.01	.045
71	China Sea	do	1,300	1,140	.88	.042

THEORY FOR THE DECAY OF WAVES

Energy Budget

fter the waves have left the generating area y travel through a region of calm where the d velocity is small compared to the wave ocity. The waves receive no energy by normal ssure but, on the contrary, they meet an air stance. The loss of energy due to the air stance, according to (30b), equals

$$R_N=-\frac{1}{2}s\rho'k^2a^2C^3=-\frac{1}{8}s\rho'g^2H^2C^{-1} \qquad (84)$$

e transfer of energy due to tangential stress (37) be neglected:

$$R_T=0 \qquad (84)$$

erefore, from equation (57)

$$R_H=-\left(1+\frac{r}{\alpha}\right)R_N,\ R_C=\frac{r}{\alpha}R_N \qquad (86a, b)$$

the decay of waves is derived from (86) without any further assumptions.

Wave period and distance from the generating area.—Substitution of (49a), (50a), and (84) in equation (86b) gives

$$\frac{1}{2}E\frac{dC}{dx}=\frac{r}{\alpha}\frac{1}{8}s\rho'g^2H^2C^{-1}$$

From (4), (6), and (78), again writing $A=2\gamma^2\rho'/\rho$, one obtains

$$\frac{dC}{dx}=2AgrC^{-1},\ \frac{dT}{dx}=\frac{8\pi^2}{g}ArT^{-1} \qquad (87)$$

Integrating from $x=F$ (end of fetch) to $x=F+D$ (end of decay distance):

$$\frac{T_D}{T_F}=\sqrt{1+16\pi^2Ar\left(\frac{D}{gT_F^2}\right)} \qquad (88)$$

where T_D and T_F are the wave periods in seconds, respectively, at the end of the decay distance and at the end of the fetch.

Travel time and distance from a generating area.—To obtain the travel time, t_D, from the end of the fetch to the end of the decay distance, it is assumed that the disturbance travels at half the wave velocity. The significance of this assumption is examined in the next section. It follows

$$t_D=\int_F^{F+D}\frac{dx}{C/2}=\frac{4\pi}{g}\int_F^{F+D}\frac{dx}{T} \qquad (89)$$

According to (87)

$$\frac{dx}{T}=\frac{g}{8\pi^2 Ar}dT$$

and

$$\frac{t_D}{T_F}=\frac{1}{2\pi Ar}\left(\frac{T_D}{T_F}-1\right) \qquad (90)$$

Wave height and distance from a generating area.—From equation (86a), considering that $dE/E=2dH/H$, one obtains

$$\frac{1}{H}\frac{dH}{dx}=-(r+\alpha)A\frac{4\pi^2}{g}T^{-2} \qquad (91)$$

Substituting for T from (87):

$$\frac{dH}{H}=-\frac{r+\alpha}{2r}\frac{dT}{T}$$

and integrating again from $x=F$ to $x=F+D$

$$\frac{H_D}{H_F}=\left(\frac{T_D}{T_F}\right)^{-\frac{r+\alpha}{2r}}$$

Equations (88), (90), and (92) are present figure 12, the nondimensional decay graph.

Intensity and distance of storm from which comes.—Sometimes it is desirable to esti properties of the storm from wave observa in the decay region. Equations (88), (90), (92) are not suitable because the unknow and T_F appear on both sides of the equa Rearranging terms and solving for D, t_D, an in terms of the observed quantities H_D, T_D,

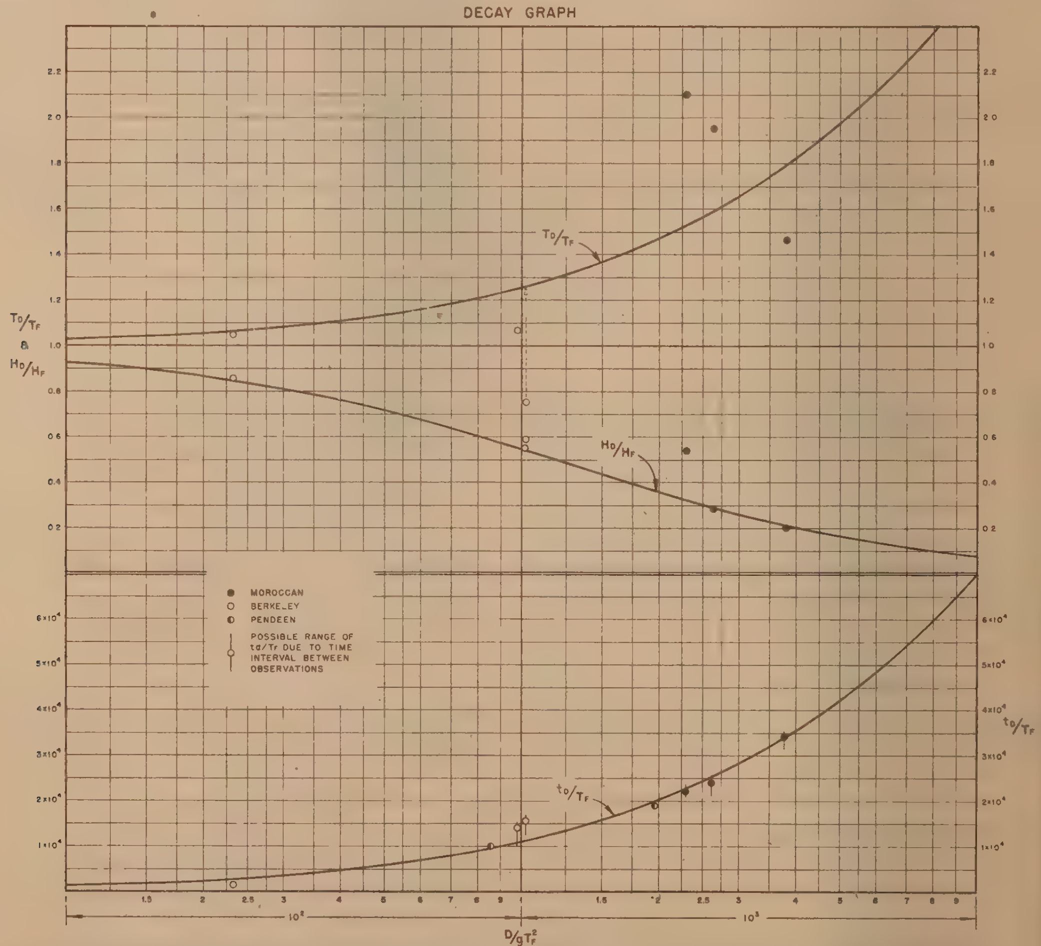


Figure 12.—Period and height of swell at end of distance of decay, and travel time represented by nondimensional parameters. Theoretical relationships shown by curves; observations by symbols.

ng into account that $\delta=H/L=2\pi H/gT^2$, one ins:

$$\frac{D}{gT_D^2}=\frac{1}{16\pi^2Ar}\left[1-\left(\frac{\delta_D}{\delta_F}\right)^{\frac{4r}{5r+\alpha}}\right] \tag{93}$$

$$\frac{t_D}{T_D}=\frac{1}{2\pi Ar}\left[1-\left(\frac{\delta_D}{\delta_F}\right)^{\frac{2r}{5r+\alpha}}\right] \tag{94}$$

$$\frac{U^2}{gH_D}=\frac{1}{2\pi}\,\frac{1}{\delta_F\beta_F^2}\left(\frac{\delta_F}{\delta_D}\right)^{\frac{r+\alpha}{5r+\alpha}} \tag{95}$$

ven in this form the equations are not satisory because it is impossible to eliminate all ınknowns. The parameters β_F and $\delta_F=f(\beta_F)$ ar on the right-hand side of the equations h relate decay distance, travel time, and wind ity to the observed quantities H_D and T_D, the unknown quantity β_F.

order to use equations (93) to (95) it is ssary to assume values of β_F. This can be by assuming a relationship between wind ity and duration based on the common rience that high winds are usually of short tion while weaker winds may blow for a time. Such a relationship determines β_F use when t and U are known the parameter can be computed and β_F read from figure 7. gure 13 two specific relationships are shown e inset, and in the upper and the lower parts e figure the corresponding values of D, t_D, U are represented as functions of the height period of the swell, H_D and T_D.

comparison of values read off from the two of figure 13 reveals that long period, high can occur only if the wind duration in the ating area has been long. Thus, a wind of ity 20 m/sec and duration 24 hours (curve set) gives a swell of period 16 seconds and t 2 feet at a distance of 2,800 km. (upper of fig. 13), but if the duration were only 12 (curve B, inset) the swell at a distance of km. would have a period of 14.8 seconds a height of only 0.9 feet. It is also found for given values of H_D and T_D conclusions distance of decay and travel time can be n with greater certainty than conclusions as nd velocity in the generating area.

The Energy Front

e preceding discussion deals with steady conditions in the area of decay. At any locality in the area of decay significant waves will attain their maximum steady state height after waves have been emitted from the area of generation for a long time. Wave heights will be lower at an earlier time, when the waves advance into an area of decay which is relatively undisturbed. The time required to reach, for example, 50 or 90 percent of the wave height corresponding to steady state conditions must be found from a study of the transient state.

Consider the fundamental equations (13) or (48a) as applied to the simple case of waves in vacuum, traveling with constant wave velocity in a nonviscous fluid:

$$\frac{\partial E}{\partial t}+\frac{\partial}{\partial x}(VE)=0 \tag{13}$$

This hypothetical case is dealt with in an earlier section of this paper (p. 6). Equation (27) which is a solution of (13) gives the wave height at any given time and distance from the generating area with good approximation. According to (27) the wave height increases from a minute percentage to very nearly 100 percent of its maximum value within a very short distance (fig. 3). The "region of sharp increase in wave height" has at any instant traveled only half as far as the leading wave; its velocity is half the velocity of the leading wave. For purposes of forecasting, therefore, the rate at which the disturbance advances in the area of calm should be taken at one-half the wave velocity, since waves further advanced than the center wave are very low.

The following numerical example will serve as illustration. Let waves of 10-m. height and 12-sec. period be generated in a storm area 4,000 km. from the point of observation. According to figure 12 the wave height at 4,000 km. will have decreased to 270 cm., the wave period will equal 19.5 sec., and the "center wave" will arrive about 90 hours after the first waves left the generating area. According to equation (27) a height equal to 10 percent of the steady-state wave height, or 27 cm., will be attained 295 wave periods, or 96 minutes, before the arrival of the central wave; a height of 242 cm., 90 percent of the steady-state wave height, will be attained 112 periods or 36 minutes after the arrival of the "center wave." Therefore, the wave height increases from 10 to 90 percent of its maximum value in 96+36 minutes, or in about 2¼ hours, while it took 90 hours for the "center wave" to arrive.

So far, a hypothetical case has been treated for which a sudden increase from zero to full wave

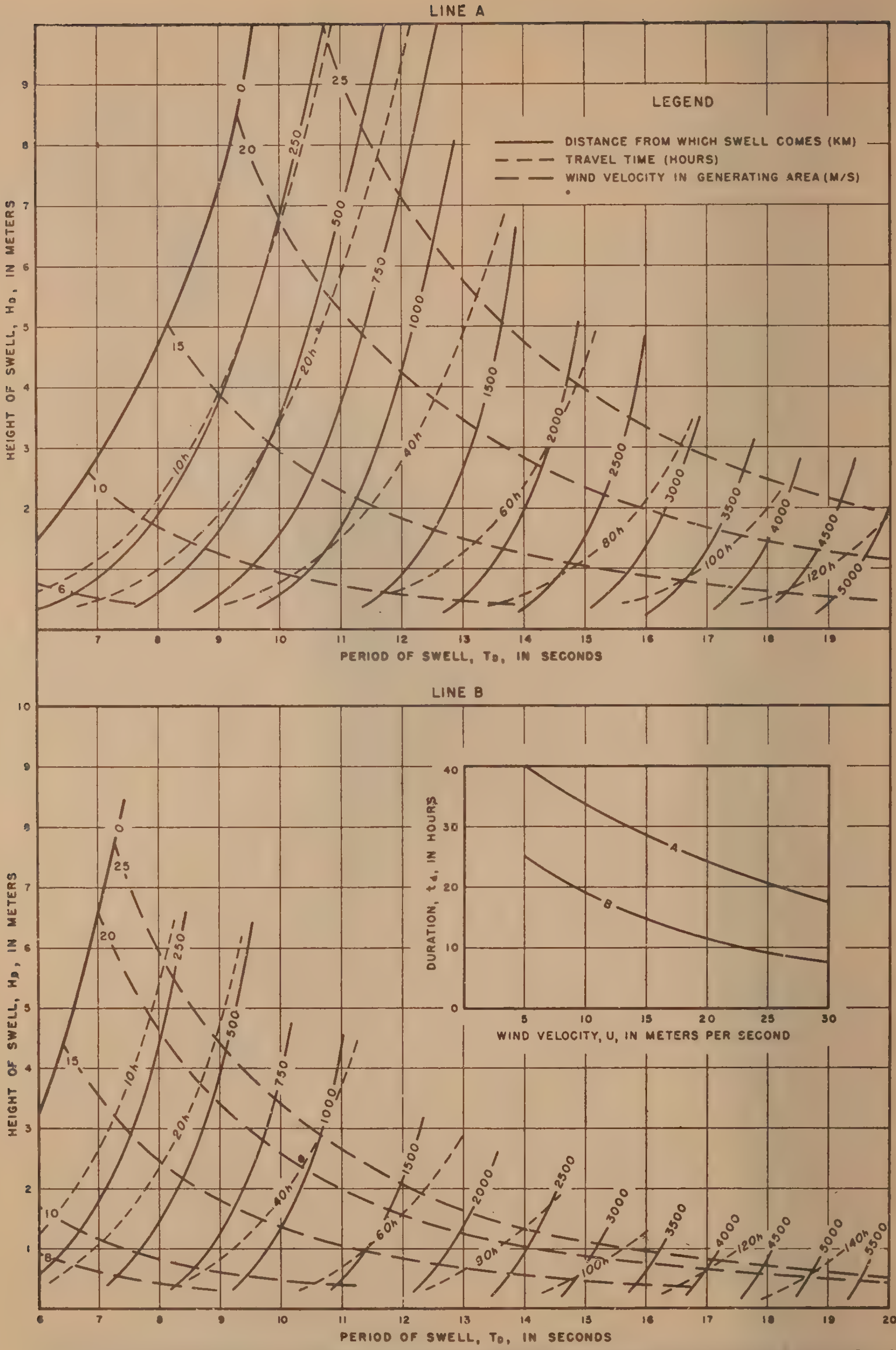


Figure 13.—Distance from which swell comes, travel time, and wind velocity in fetch as functions of height and period at swell at end of distance of decay for two assumed relationships between wind velocity in fetch and duration.

t has been assumed at the end of the generat-
rea. Actually, this increase will not be sud-
ut will depend upon the fetch and the wind
ity (see figs. 6 and 7). It has been shown
the sudden increase in wave height at the
of the generating area retains much of its
ness as the disturbance travels through the
of decay; it is reasonable to assume, therefore,
a gradual increase at the end of the fetch will
ar as a similar gradual increase in wave
t at any point in the area of decay.

a storm should increase in violence, then
and long waves may arrive simultaneously
or may overtake lower and slower waves
were generated at an earlier time. If the
r waves overtake the lower and slower waves,
re abrupt increase of wave height can be
ted at large distances from the generating

e inconsistency remains to be explained.
rding to equation (12), the wave period re-
s constant near a geometric point travelling at half the wave velocity. Therefore no increase in wave period should be observed at the energy front, and only the low waves arriving ahead of the energy front should have periods larger than the ones at the end of the fetch. Observations do indicate, however, that the period of the significant waves increases with distance from the generating area.

The explanation can probably be found in the limitations imposed by the Stokes theory, and by the assumption of the constant wave velocity made in the section dealing with the propagation of a disturbance through a region previously undisturbed. Rossby (1945) has shown that for his generalized Stokes waves a dispersion of energy from short-period to long-period waves does, indeed, take place. At present it has not been found possible to take some of these recent theoretical studies into account when dealing with significant waves in the decay region, but the theory presented here, although incomplete, has been found consistent with observations.

OBSERVATIONS OF THE DECAY OF WAVES

tle factual infomation is available concern-
he behavior of waves which are no longer
ct to wind action. It appears that the wave
d and, therefore, the wave length continues
crease while the wave height decreases, and
these changes contribute toward reducing
vave steepness. Furthermore, shorter waves
y much more rapidly than longer waves, and
e area of calm the irregular pattern of steep
waves is transformed into a pattern of regular,
ndulations known as swell.

anges in wave characteristics with distance
the generating area depend also upon the
d of the wave at the end of the generating
No observations are available from which
ese factors can be derived. A rough check of
heory can be obtained by plotting in figure 12
ondimensional ratios of (88), (90), and (92) as
ed from observed values of T_D, t_D, and H_D and
s of H_F and T_F computed from weather maps.
validity of such a check rests upon the assump-
that the relationships in the generating area
vell established (figs. 6 and 7) and that the
her situations have been analyzed correctly.
rvations at two widely separated localities in
egion of decay are desirable for a study of the
y of waves without reference to the processes
neration.

Wave height and distance from generating area.—Six observations have been plotted in figure 12. Three observations marked "MOROCCO" were taken by the French Meteorological Service. These consisted of wave height and period about three times daily. The points in figure 12 represent averages of observations at Casablanca, Rabat, and Mehedya. Three observations marked "BERKELEY" were taken from weather ships, and for those the distance of decay is somewhat shorter. The agreement between theory and observations is fair.

The following quotation from the British forecasting report is of interest (British Admiralty 1942):

> But as the forces mentioned in the first paragraph as acting on the surface now act against the motion of the water, energy is continuously removed from the waves and their height diminishes. The rate of diminution of height is greater for the shorter waves; it appears, from such evidence as is available, that the waves lose roughly one-third of their height each time they travel a distance in miles equal to their length in feet, e. g., a swell 600 feet long and 30 feet high is 20 feet high after 600 miles, 13.3 feet high after 1,200 miles, 9 feet high after 1,800 miles, 6 feet high after 2,400 miles, and so on.

According to this rule:

$$\frac{H_D}{H_F}=0.67 \text{ for } \frac{D}{L_F}=6{,}080 \text{ or } \frac{D}{gT_F^2}=\frac{6{,}080}{2\pi}=975,$$

and a comparison can be made with the curve in figure 12. One obtains:

D/L_F (D in miles, L_F in feet)	1	2	3	4	5
Dg/T_F^2	975	1, 950	2, 920	3, 900	4, 900
H_D/H_F British rule	0. 67	0. 44	0. 30	0. 20	0. 13
H_D/H_F Fig. 12	. 55	. 37	. 27	. 21	. 17

The values of H_D/H_F agree for $D/L_F=4$. Assuming T_F equal to 8 seconds, the distance of decay equals 1,300 nautical miles. For smaller distances of decay, the British rule gives larger wave heights, for longer distances, smaller wave heights, but the general agreement is quite satisfactory.

Travel time and distance from the generating area.—In additon to the Morocco and Berkeley observations, two observations at Pendeen, England, have been included. The character of the observation at Pendeen will be discussed further when dealing with wave periods. In determining the arrival time, attention was focused on an abrupt change in observed height of swell, usually a peak. At Pendeen records of the swell were obtained at intervals of 2 hours and the arrival time of the peak could be accurately established. In the other examples, for which observations were widely spaced, the possible error in arrival time is indicated by the length of the line drawn through the point of observation. The agreement between theory and observations is remarkably good.

Certain observations by Berkeley, where the winds decreased gradually, have been omitted and only observations where the duration was fairly definite are included in figure 12. Among the omitted observations there was some evidence that the theoretical travel time was too long. The problem of travel time warrants further theoretical study and examination of reliable, continuous observations.

Wave period and distance from the generating area.—The observed period increase confirms the order of magnitude of the theoretical period increase, but individual points are too scattered to draw any further conclusions. Since the period increase is implicitly contained in the relationship dealing with travel time and, to a lesser extent, in the relationship dealing with wave height, the fair agreement between theory and observations for these quantities may be regarded as indirect evidence in favor of the theoretical relationship for wave period.

The scatter of the observations is partly due to the fact that in the ratio, T_D/T_F, both numerator and denominator are subject to considerabl certainty. This uncertainty arises becaus servations of period are difficult and becau given localities the periods are not constan vary over wide limits.

Observations at Pendeen are well suited to s the increase in wave period. They were ma means of a pressure recorder placed at a dep about 100 feet and were subjected to a harn analysis by means of specially designed equip Twenty-minute records at two-hourly inte were examined for two periods, March 14 and April 17 to 19, 1945. For these two pe the weather situations were similar, each characterized by one well defined low-pre system traveling toward NE across the N Atlantic. Both storms could be expecte produce heavy swell that would reach Pen from nearly the same direction.

In the upper parts of figures 14 and 15 the r of the periods recorded at Pendeen are show the bands enclosed between the full-drawn the dashed lines. The full-drawn lines inclu recorded periods, the dashed lines include the frequent ones. The reason for the great bility of the observed periods is probably waves arriving at Pendeen did not come fr "line source" but from different portions of a generating area and had used different travel over different distances of decay.

The computed periods at the end of the are indicated by the lower circles and the for wave periods at Pendeen by the circles di above them. The numbers indicate the t time from the end of the fetch to Pendeen. computed fetch at the ends of the periods ar arranged in chronological order because s times waves which left the fetch earlier than waves arrived at Pendeen at a later time. forecast periods generally lie inside the ba observed periods except on March 14 and on March 15 and on April 18, when the "forerunner" of the swell appeared at Pen These initial waves were low and may repr swell arriving ahead of the energy front.

The forecast height in feet and the obs height on an arbitrary scale are also shown i lower parts of figures 14 and 15. The chang computed and observed heights are in good a ment. The peaks in the figures have been to check the theoretical travel time and are s by the points marked "PENDEEN" in figu

The concept of an increasing wave period i

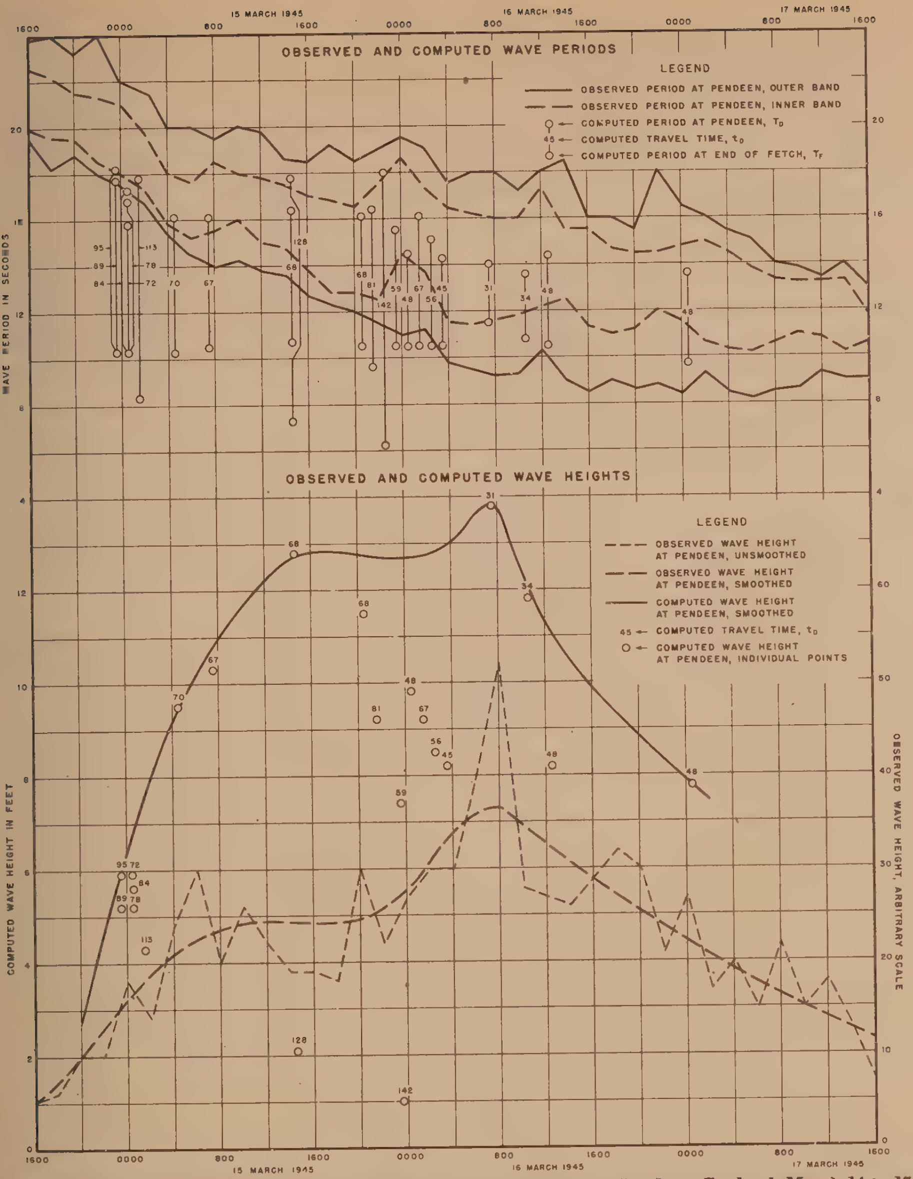


Figure 14.—Observed and computed wave periods and wave heights at Pendeen, England, March 14 to 17, 1945. For explanation see text.

n of decay has long been a controversial ect. According to the classical theory waves ld proceed with constant velocity into the of calm as long as the depth to the bottom ins greater than about one-half the wave h. In recent years Cornish (1934) has hasized that such is the case. He has quoted mber of examples to show that the periods ell observed on coasts were in agreement with ds which might have been produced by strong s over the adjacent ocean. However, in the ssion dealing with observations of wave velocities and wind velocities Cornish has overestimated wave periods in the generating area since he has paid attention only to the maximum wind velocity. He has omitted any discussion of the length of time the strong wind blew in a uniform direction, as well as any estimate of the fetch of the wind. Since these factors are of great importance, Cornish's arguments lose much of their weight.

Krümmel (1911) compiled considerable evidence to show that the swell has longer periods than the originally produced waves and therefore, corre-

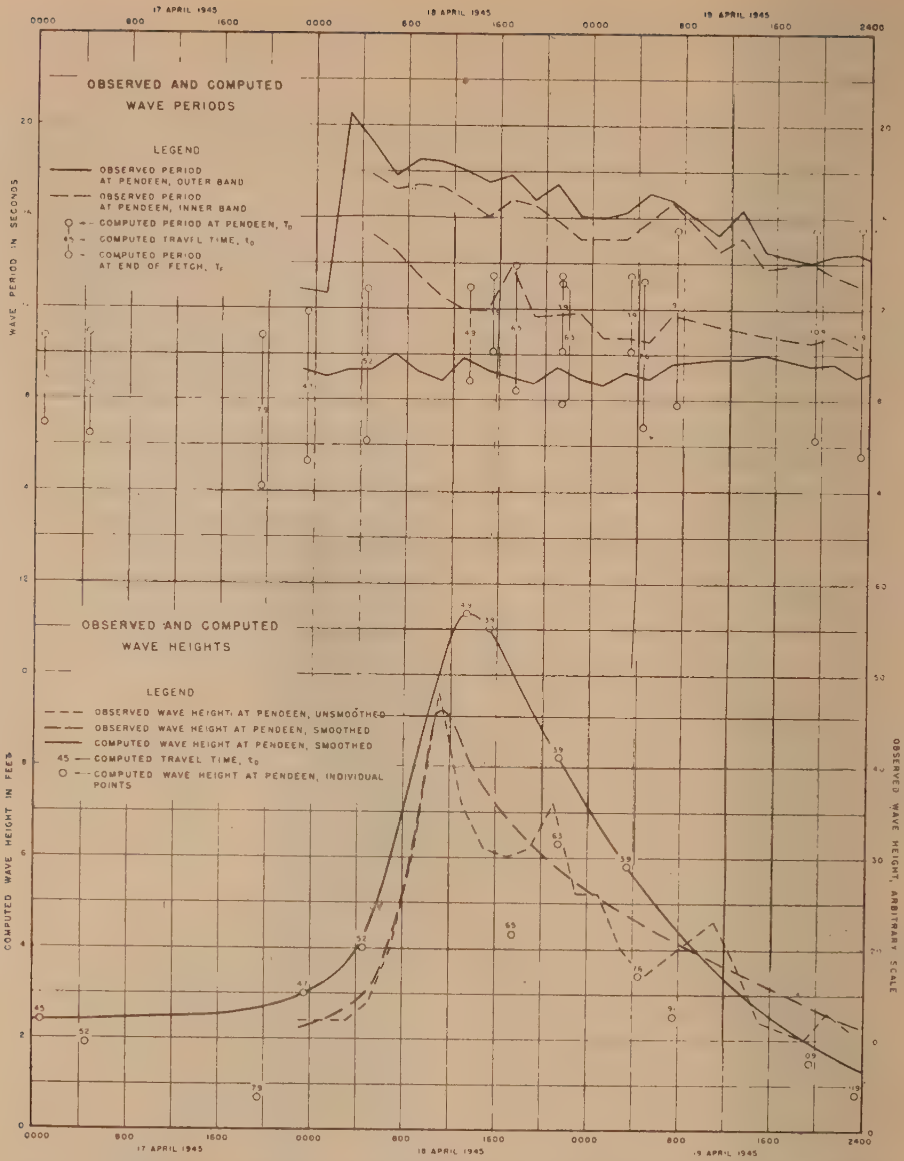


Figure 15.—Observed and computed wave periods and wave heights at Pendeen, England, April 17 to 19, 1945. For explanation see text.

spondingly greater velocity of progress and greater length. He quotes (1911, p. 94) one particular instance in the Atlantic Ocean when swell from one source was observed by a number of vessels which reported longer and longer periods the greater their distance from the source. At a distance of 6,700 km. from the source the period had increased by a factor of 1.7. Krümmel therefore concluded that the waves increase in period, velocity of progress, and length as they move away from their source.

This conclusion is substantiated by an exa
tion of the frequencies of different wind vel
over the North Pacific and the North At
and of the frequencies of swell of different p
on the coasts of southern California and of
west Africa. Table 5 shows the periods of
produced by different wind velocities and
durations. The wave heights and period
wind durations of 20, 30, and 40 hours, are
from the curves in figure 7 which are based
theoretical considerations but which have

to be in agreement with empirical evidence.

Table 5

ve Periods for Wind of Given Velocities and Duration

Wind velocity		Wave periods, seconds		
eaufort scale	m/sec	20 hours	30 hours	40 hours
4	5.3– 8.5	3.9– 4.9	4.5– 5.9	5.0–6.5
5	8.6–11.0	5.0– 5.9	6.0– 6.9	6.6–7.7
6	11.1–14.1	6.0– 6.9	7.0– 8.0	7.8–9.0
7	14.2–17.2	7.0– 7.8	8.1– 9.2	-------
8	17.3–20.8	7.9– 8.8	9.3–10.3	-------
9	20.9–24.4	8.9– 9.7	10.4–11.4	-------
10	24.5–28.5	9.8–10.7	---------	-------
11	28.6–32.7	10.8–11.6	---------	-------

ording to the Atlas of Climatological Charts e Oceans (U. S. Weather Bureau, 1938), velocities exceeding 7 Beaufort are not nt over the oceans. For the stormy part of orth Pacific in winter the frequency of such vind velocities exceeds 15 percent in only a gions, and in the North Atlantic it reaches rcent in only one area. The duration of winds is usually between 20 and 30 hours. fore, waves of periods longer than 8.9 ls would not be produced on more than 15 to cent of the days in winter; waves of periods ling 12 seconds would never be formed se wind velocities of 10 to 11 Beaufort occur and are of short duration. It follows that waves proceeded without change in period riods of the swells on the coasts of southern rnia and of northwest Africa would exceed 8.9 seconds in 15 to 25 percent of the cases and would never exceed 12 seconds.

Gutenberg (1929) has commented upon the problem of the increase of wave period and calls it a truly geophysical phenomenon noticeable only over long distances and periods of time. He finds that earthquake waves, microseismic and ordinary sound waves increase in period in a manner similar to the one characteristic of water waves. For seismic waves the increase might be associated with the internal viscosity of the transmitting medium.

Although the "kinematics" of the increase in wave period is now fairly well understood, due mostly to studies by Rossby (1945), the physical causes of the phenomenon remain obscure. The explanation may lie in an analogy with the Cauchy-Poisson problem of impulsive wave generation (Lamb, 1932, p. 384). Due to the impulsive generation a spectrum of wave periods is present at all times and the longer and faster waves will run ahead of the shorter and slower waves. The entire wave train stretches, resulting in an increase of wave period. However, the Cauchy-Poisson problem deals with a momentary generation of waves as, for example, waves caused by a pebble dropped in water. In storm areas the process of wave formation must be a semicontinuous one and it represents a much more difficult problem. This paper may serve to clarify the relationships between wind, sea, and swell, but it leaves a number of fundamental questions unanswered.

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APPENDIX I

o prove that

$$ {}^{n}R_{m}=\frac{n!}{2^{n}}\sum_{r=0}^{r=n-m}\frac{1}{r!(n-r)!} \tag{22} $$

lution to the difference equation

$$ {}^{n+1}R_{m}-\frac{1}{2}{}^{n}R_{m}-\frac{1}{2}{}^{n}R_{m-1}=0 \tag{25} $$

tuting (22) into (25)

$$ \frac{(n+1)!}{2^{n+1}}\sum_{r=0}^{r=n+1-m}\frac{1}{r!(n+1-r)!}-\frac{n!}{2\times 2^{n}}\sum_{r=0}^{r=n-m}\frac{1}{r!(n-r)!}-\frac{n!}{2\times 2^{n}}\sum_{r=0}^{r=n+1-m}\frac{1}{r!(n-r)!}=0 $$

plying by $2^{n+1}/n!$, bringing all terms on a common denominator, and combining the first ird terms, one obtains

$$ \sum_{r=0}^{r=n+1-m}\frac{r}{r!(n+1-r)!}-\sum_{r=0}^{r=n-m}\frac{n+1-r}{r!(n+1-r)!}=0 $$

$$ \frac{1}{(n-m)!(m)!}+\sum_{r=0}^{r=n-m}\frac{2r-(n+1)}{r!(n+1-r)}=0 \tag{I} $$

quation (I) is satisfied for any values of n and m, as will be proven by the method of mathe- l induction. First, it will be shown to hold for $n-m=0$, $n-m=1$, and $n-m=2$. Then it e shown that if we assume (I) to hold for $n-m=k$, it must also hold for $n-m=k+1$, and for any value of $n-m$.

$-m=0$, $m=n$:

$$ \frac{1}{0!m!}=\frac{n+1}{0!(n+1)!}=\frac{1}{n!}-\frac{1}{n!}=0 $$

$-m=1$, $m=n-1$:

$$ \frac{1}{1!(n-1)!}-\frac{n+1}{0!(n+1)!}+\frac{2-(n+1)}{1!n!}=\frac{1}{(n-1)!}-\frac{1}{n!}+\frac{1-n}{n!}=\frac{n}{n!}-\frac{1}{n!}+\frac{1-n}{n!}=0 $$

$-m=2$, $m=n-2$:

$$ \frac{1}{2!(n-2)!}-\frac{1}{n!}+\frac{1-n}{n!}+\frac{3-n}{2(n-1)!}=\frac{n-1}{2(n-1)!}-\frac{1}{(n-1)!}-\frac{(n-3)}{2(n-1)!}=\frac{n-1}{2(n-1)!}-\frac{n-1}{2(n-1)!}=0 $$

$-m=k$, $m=n-k$:

$$ \frac{1}{k!(n-k)!}+\sum_{r=0}^{r=k}\frac{2r-(n+1)}{r!(n+1-r)}=0 \tag{II} $$

$-m=k+1$, $m=n-k-1$:

$$ \frac{1}{(k+1)!(n-k-1)!}+\sum_{r=0}^{r=k+1}\frac{2r-(n+1)}{r!(n+1-r)!}=\frac{n-k}{(k+1)!(n-k)!}+\sum_{r=0}^{r=k}\frac{2r-(n+1)}{r!(n+1-r)!}+\frac{2(k+1)-(n+1)}{(k+1)!(n-k)!}= $$

$$ \frac{n-2k-1}{(k+1)!(n-k)!}-\frac{n-2k-1}{(k+1)!(n-k)!}\ \text{(in view of Equation II)}=0 $$

q. e. d.

APPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA

Table I

WAVE AGE, β, AND STEEPNESS, δ

No.	Wind velocity, U (m/sec)	Wave velocity, C (m/sec)	Wave length, L (m)	Wave height, H (m)	Wave age $\beta = C/U$ (ratio)	Wave steepness, $\delta = H/L$ (percent)	Reference*	Legend used in fig. 5
1	8.8	16.4	172	2.2	1.87	1.3		Berkeley
2	11.3	16.4	172	2.7	1.44	1.6		do
3	11.3	16.6	175	2.9	1.46	1.7		do
4	17.0	22.6	328	5.5	1.33	1.7	X (1923)	Zimmermann
5	10.8	17.0	186	3.2	1.57	1.7		Berkeley
6	19.0	22.8	336	6.0	1.20	1.8	Z (1923)	Zimmermann
7	17.0	26.8	461	8.5	1.58	1.8	Z (1923)	do
8	7.0	11.1	79	1.5	1.58	1.9	Z (1923)	do
9	5.0	8.9	50	1.0	1.78	2.0	Z (1923)	do
10	17.0	20.5	270	5.5	1.21	2.0	Z (1923)	do
11	6.7	9.4	56	1.2	1.40	2.1		U. S. S. *Augusta*
12	12.9	20.3	264	6.1	1.57	2.3		H. M. S. *Forrester*
13	17.0	18.2	214	5.0	1.07	2.3	Z (1923)	Zimmermann
14	12.9	15.6	156	3.7	1.21	2.4		H. M. S. *Forrester*
15	5.0	8.9	51	1.2	1.78	2.4	Z (1923)	Zimmermann
16	6.0	8.1	42	1.0	1.35	2.4	Z (1923)	do
17	6.7	7.8			1.16	2.4	Sc (1939)	Meteor
18	6.2	6.2	25	.6	1.00	2.4		U. S. S. *Augusta*
19	5.7	6.3	25	.6	1.10	2.4		do
20	12.9	12.5	100	2.4	.97	2.4		do
21	12.9	12.5	100	2.4	.97	2.4		do
22	10.0	12.5	100	2.5	1.25	2.5	Z (1923)	Zimmermann
23	11.3	14.1	135	3.4	1.24	2.5		Berkeley
24	5.0	8.6	47	1.2	1.72	2.6	Z (1923)	Zimmermann
25	9.3	13.1	110	2.8	1.41	2.6		Berkeley
26	10.8	12.5	100	2.6	1.16	2.6		U. S. S. *Augusta*
27	5.0	8.4	45	1.2	1.68	2.7	Z (1923)	Zimmermann
28	14.0	14.1	127	3.5	1.01	2.8	Z (1923)	do
29	9.8	10.9	76	2.1	1.11	2.8		U. S. S. *Augusta*
30	5.0	8.1	42	1.2	1.62	2.9	Z (1923)	Zimmermann
31	15.0	17.0	185	3.5	1.13	2.9	Z (1923)	do
32	9.4	8.6			.93	2.9	Sc (1939)	Meteor
33	5.9	11.2			1.90	2.9	K (1911)	Paris
34	7.2	12.6			1.75	2.9	K (1911)	do
35	15.0	19.2	237	7.0	1.28	3.0	Z (1923)	Zimmermann
36	16.0	19.8	235	7.0	1.20	3.0	K (1911)	Paris
37	11.3	10.9	76	2.3	.96	3.0		U. S. S. *Augusta*
38	9.3	10.9	76	2.3	1.17	3.0		U. S. S. *Augusta*
39	8.6	12.4			1.44	3.0	K (1911)	Paris
40	17.0	16.1	165	5.0	.95	3.0	Z (1923)	Zimmermann

See footnotes at end of table.

Table I—Continued

WAVE AGE, β, AND STEEPNESS, δ—Continued

Wind velocity, U (m/sec)	Wave velocity, C (m/sec)	Wave length, L (m)	Wave height, H (m)	Wave age $=\beta C/U$ (ratio)	Wave steepness, $\delta=H/L$ (percent)	Reference*	Legend used in fig. 5	Manner of measurement†
7.0	9.0	45	1.4	1.22	3.1	G (1935)	Gassenmayr	c
13.0	14.0	140	4.4	1.12	3.1	G (1935)	do	e
13.0	13.2	111	3.5	1.01	3.2	Z (1923)	Zimmermann	f
19.0	19.2	237	7.5	1.01	3.2	Z (1923)	do	f
8.2	10.9	76	2.4	1.33	3.2		U. S. S. *Augusta*	a
8.0	8.6	47	1.5	1.08	3.2	Z (1923)	Zimmermann	f
12.4	14.0			1.13	3.2	K (1911)	Paris	c
9.8	10.9	76	2.4	1.11	3.2		Berkeley	a
13.0	16.3	171	5.5	1.25	3.2	Z (1923)	Zimmermann	f
7.7	9.4	56	1.8	1.22	3.3		U. S. S. *Augusta*	a
6.0	8.4	45	1.5	1.40	3.3	Z (1923)	Zimmermann	f
7.0	9.6	59	2.0	1.37	3.4	Z (1923)	do	f
10.3	7.8	39	1.4	.76	3.5		U. S. S. *Augusta*	a
17.0	15.6	156	5.5	.92	3.6	Z (1923)	Zimmermann	f
11.0	11.0	78	2.8	1.00	3.6	Z (1923)	do	f
14.0	13.1	110	4.0	.94	3.6	Z (1923)	do	f
7.0	7.2	33	1.2	1.03	3.6	Z (1923)	do	f
5.2	6.2	25	.9	1.19	3.6		U. S. S. *Augusta*	a
15.0	15.1	147	5.5	1.01	3.8	Z (1923)	Zimmermann	f
14.0	15.0	120	4.5	1.08	3.8	G (1935)	Gassenmayr	e
6.0	8.0	40	1.5	1.25	3.8	G (1935)	do	e
10.8	9.4	56	2.1	.87	3.8		U. S. S. *Augusta*	a
12.9	15.6	156	6.1	1.21	3.9		H. M. S. *Forrester*	a
9.0	7.0	35	1.4	.78	4.0	G (1935)	Gassenmayr	e
10.0	8.0	40	1.6	.80	4.0	G (1935)	do	e
11.0	12.4	99	4.0	1.13	4.0	Z (1923)	Zimmermann	f
13.0	13.9	123	5.0	1.07	4.1	Z (1923)	do	f
12.0	13.9	123	5.0	1.16	4.1	Z (1923)	do	f
17.0	14.5	134	5.5	.85	4.1	Z (1923)	do	f
11.0	9.5	57	2.4	.85	4.2	G (1935)	Officers U. S. Navy	b
13.0	11.4			.88	4.2	K (1911)	Paris	c
14.0	12.8	105	4.5	.91	4.3	Z (1923)	Zimmermann	f
6.0	5.5	20	.85	.92	4.3	E (1940)	Ehring	a
11.0	9.4	56	2.5	.85	4.5	Z (1923)	Zimmermann	f
14.9	15.0			1.01	4.5	K (1911)	Paris	c
17.0	13.1	110	5.0	.77	4.6	Z (1923)	Zimmermann	f
14.0	11.7	88	4.0	.84	4.6	Z (1923)	do	f
23.0	18.3	214	9.8	.78	4.6	S (1893)	Schott	a
10.0	10.3	68	3.2	1.04	4.7	S (1893)	do	a
17.0	17.0	185	9.0	1.00	4.8	Z (1923)	Zimmermann	f

ootnotes at end of table.

APPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA—Continue

Table I—Continued

WAVE AGE, β, AND STEEPNESS, δ—Continued

No.	Wind velocity, U (m/sec)	Wave velocity, C (m/sec)	Wave length, L (m)	Wave height, H (m)	Wave age $\beta=C/U$ (ratio)	Wave steepness, $\delta=H/L$ (percent)	Reference*	Legend used in fig. 5
81	17.0	10.2	64	3.2	.61	5.0	G (1935)	Officers U. S. Navy
82	9.0	6.7	30	1.5	.79	5.0	G (1935)	Gassenmayr
83	9.0	7.8	39	2.0	.91	5.1	S (1893)	Schott
84	18.0	13.7	121	6.2	.74	5.2	S (1893)	do
85	23.0	19.7	248	13.0	.86	5.2	Z (1923)	Zimmermann
86	6.0	6.2	25	1.3	1.03	5.2	G (1935)	Gassenmayr
87	23.0	12.7	140	7.5	.54	5.4	G (1935)	do
88	21.0	20.2	262	14.0	.97	5.4	Z (1923)	Zimmermann
89	20.0	12.0	120	6.5	.60	5.4	G (1935)	Gassenmayr
90	21.0	18.5	218	12.0	.88	5.5	Z (1923)	Zimmermann
91	17.0	15.1	145	8.0	.89	5.5	Z (1923)	do
92	14.4	9.4	56	3.1	.65	5.5	----------	H. M. S. *Forrester*
93	16.0	13.3	113	6.0	.83	5.5	K (1911)	Paris
94	16.5	3.6	8	.45	.22	5.6	----------	Gibson
95	11.0	8.4	45	2.5	.76	5.6	S (1893)	Schott
96	11.0	8.4	45	2.5	.76	5.6	Z (1923)	Zimmermann
97	10.0	8.4	45	2.5	.84	5.6	Z (1923)	do
98	14.0	11.5	98	5.5	.83	5.6	G (1935)	Officers U. S. Navy
99	11.0	6.7	40	2.3	.61	5.7	G (1935)	Gassenmayr
100	11.0	6.2	40	2.5	.55	6.2	G (1935)	do
101	16.0	12.9	107	6.7	.83	6.2	C (1934)	Cornish
102	17.0	12.5	100	6.4	.74	6.4	G (1935)	Officers U. S. Navy
103	12.9	9.4	56	3.7	.73	6.6	----------	H. M. S. *Forrester*
104	11.0	9.4	56	3.7	.84	6.6	S (1893)	Schott
105	11.0	8.0	45	3.0	.73	6.6	G (1935)	Gassenmayr
106	23.0	12.0	113	7.6	.52	6.7	G (1935)	Officers U. S. Navy
107	16.0	4.5	13	.9	.28	6.9	----------	Gibson
108	20.0	14.2	129	9.0	.71	7.0	S (1893)	Schott
109	17.0	14.6	137	10.0	.86	7.3	Z (1923)	Zimmermann
110	20.0	13.3	113	8.3	.67	7.4	S (1893)	Schott
111	20.0	8.5	80	6.0	.43	7.5	G (1935)	Gassenmayr
112	26.0	12.0	92	6.9	.46	7.5	C (1934)	Cornish
113	14.0	9.5	58	4.5	.68	7.5	Z (1923)	Zimmermann
114	25.0	1.6	1.7	.13	.06	7.7	C (1934)	Cornish
115	25.0	5.6	20	1.5	.22	7.7	C (1934)	do
116	11.0	5.8	35	2.7	.52	7.7	G (1935)	Gassenmayr
117	17.0	6.4	45	3.5	.38	7.7	G (1935)	do
118	8.8	6.2	25	2.0	.71	8.0	----------	U. S. S. *Augusta*
119	9.6	5.4	18	1.5	.56	8.3	----------	Dover
120	8.2	6.7	29	2.4	.82	8.3	----------	U. S. Engineers

See footnotes at end of table.

PPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA—Continued

Table I—Continued

WAVE AGE, β, AND STEEPNESS, δ—Continued

Wind elocity, U (m/sec)	Wave velocity, C (m/sec)	Wave length, L (m)	Wave height, H (m)	Wave age $\beta=C/U$ (ratio)	Wave steepness, $\delta=H/L$ (percent)	Reference*	Legend used in fig. 5	Manner of measurement†
11.0	6.8	30	2.6	.62	8.7	K (1911)	Krümmel	c
11.3	6.7	29	2.7	.59	9.3		U. S. Engineers	a
12.4	4.6	14	1.4	.37	10.0		Dover	c
23.0	13.1	110	11.0	.57	10.0	Z (1923)	Zimmermann	f
9.6	5.2	17	1.8	.54	10.6		Dover	c
12.4	4.9	15	1.7	.39	11.3		do	c
12.4	4.9	15	1.8	.39	12.0		do	c
9.8	3.8	9	1.1	.39	12.2		do	c

erence: C=Cornish; E=Ehring; G=Gaillard; K=Krümmel; S=Schott; Sc=Schumacher; Z=Zimmermann.

nner of measurement: a—C and L computed from observed T. b—C computed from observed T and L averaged. c—C computed from observed observed, L computed from observed T. e—C and L observed. f—Manner in which C, L, and T were obtained not known.

APPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA—Continu

Table II

WAVE HEIGHT AND WAVE AGE AS FUNCTIONS OF FETCH

No.	Wind velocity U (m/sec)	Wave height H (m)	Fetch F (km)	Wave velocity C (m/sec)	$\frac{gF}{U^2}$	$\frac{gH}{U^2}$	$\frac{C}{U}$	Reference*	Legend used in fig. 6
11	6.7	1.2	157	9.4	3.4×10^4	0.27	1.40	----------	U. S. S. *Augusta*
18	6.2	.6	157	6.2	4.1×10^4	.16	1.00	----------	do
20	12.9	2.4	167	12.5	9.9×10^3	.14	.97	----------	do
21	12.9	2.4	167	12.5	9.9×10^3	.14	.97	----------	do
26	10.8	2.6	232	12.5	1.9×10^4	.22	1.16	----------	do
38	9.3	2.3	167	10.9	1.9×10^4	.26	1.17	----------	do
45	8.2	2.4	167	10.9	2.4×10^4	.35	1.33	----------	do
50	7.7	1.8	167	9.4	2.8×10^4	.30	1.22	----------	do
58	5.2	.9	157	6.2	5.7×10^4	.33	1.19	----------	do
94	16.5	.5	1.3	3.6	4.7×10	.016	.22	----------	Gibson
107	16.0	.9	3.5	4.5	1.3×10^2	.032	.28	----------	do
120	8.2	2.4	363	6.7	5.3×10^4	.35	.82	----------	U. S. Engineers
122	11.8	2.7	152	6.7	1.2×10^4	.21	.59	----------	do
129	7.7	1.1	156	------	2.6×10^4	.18	------	----------	do
130	7.7	1.7	156	------	2.6×10^4	.28	------	----------	do
131	6.7	1.5	161	------	3.5×10^4	.33	------	----------	do
132	8.8	2.1	161	------	2.0×10^4	.27	------	----------	do
133	7.7	2.1	156	------	2.6×10^4	.35	------	----------	do
134	16.0	4.0	130	------	5.0×10^3	.15	------	----------	do
135	16.0	4.3	120	------	4.6×10^3	.16	------	----------	do
136	12.9	3.4	152	------	9.0×10^3	.20	------	----------	do
137	11.8	2.7	152	------	1.1×10^4	.19			do
138	9.3	2.9	156	------	1.8×10^4	.33	------	----------	do
139	6.2	.9	152	------	3.9×10^4	.23	------	----------	do
140	9.3	1.5	145	------	1.6×10^4	.17	------	----------	do
141	11.8	2.9	156	------	1.1×10^4	.20	------	----------	do
142	6.7	.9	363	------	7.9×10^4	.20	------	----------	do
143	5.7	.8	363	------	1.1×10^5	.24	------	----------	do
144	9.3	1.2	120	------	1.4×10^4	.14	------	----------	do
145	9.3	1.7	152	------	1.7×10^4	.19	------	----------	do
146	8.2	1.8	363	------	5.3×10^4	.26	------	----------	do
147	10.3	2.1	156	------	1.4×10^4	.19	------	----------	do
148	9.8	2.1	156	------	1.6×10^4	.21	------	----------	do
149	15.0	6.7	482	12.4	2.1×10^4	.29	.80	C (1934)	Cornish
150	20.6	11.0	1,112	16.5	2.5×10^4	.25	.80	C (1934)	do
151	4.0	------	.0135	.50	8.3	-----	.12	S (1937)	Stanton
152	5.0	------	.0135	.57	5.3	-----	.11	S (1937)	do
153	6.2	------	.0135	.67	3.4	-----	.11	S (1937)	do
154	7.2	------	.0135	.77	2.6	-----	.11	S (1937)	do

*C=Cornish; S=Stanton.

†See footnote of table I.

PPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA—Continued

Table III

WAVE HEIGHT AND WAVE AGE AS FUNCTIONS OF DURATION

Wind eloci-ty U m/sec)	Duration t (sec)	Wave height H (m)	Wave velocity C (m/sec)	$\frac{gt}{U}$	$\frac{gH}{U^2}$	$\frac{C}{U}$	Reference*	Legend used in fig. 7	Manner of measurement†
11.3	8.93×10^4	2.7	16.4	7.8×10^4	0.21	1.44		Berkeley	a
11.3	6.92×10^4	2.9	16.6	6.0×10^4	.22	1.46		do.	a
10.8	1.80×10^5	3.2	17.0	1.6×10^5	.27	1.57		do.	a
5.7	3.24×10^4	.6	6.3	5.6×10^4	.18	1.10		U. S. S. *Augusta*	a
11.3	9.28×10^4	3.4	14.1	8.8×10^4	.26	1.24		Berkeley	a
9.8	6.12×10^4	2.1	10.9	6.1×10^4	.21	1.11		U. S. S. *Augusta*	a
16.0	3.60×10^5	7.0	19.8	2.2×10^5	.27	1.20	K (1911)	Paris	c
11.3	5.40×10^4	2.3	10.9	4.7×10^4	.14	.96		U. S. S. *Augusta*	a
9.8	7.57×10^4	2.4	10.9	7.6×10^4	.25	1.11		Berkeley	a
10.3	3.60×10^4	1.4	7.8	3.4×10^4	.13	.76		U. S. S. *Augusta*	a
10.8	3.78×10^4	2.1	9.4	3.4×10^4	.18	.87		do.	a
16.0	8.64×10^4	6.0	13.3	5.4×10^4	.23	.83	K (1911)	Paris	c
8.8	3.06×10^4	2.0	6.2	3.4×10^4	.25	.71		U. S. S. *Augusta*	a
11.0	6.47×10^4	2.6	6.8	5.8×10^4	.21	.62	K (1911)	Krümmel	c
9.8	1.80×10^4	1.1	3.8	1.8×10^4	.11	.39		Dover	a
9.3	4.18×10^4	2.4		4.4×10^4	.27			Berkeley	a
18.5	2.51×10^4	4.4		1.3×10^4	.13			Emmons & Clarke	a

Krümmel.

†See footnote of table I.

APPENDIX II. COLLECTION OF EMPIRICAL WAVE DATA—Continued

Table IV

HEIGHT, PERIOD, AND TRAVEL TIME OF SWELL

No.	Wind velocity U (m/sec)	Fetch F (km)	Duration t_d (km)	Decay distance D (km)	Computed wave height at end of fetch H_F (m)	Computed wave period at end of fetch T_F (sec)	Observed height of swell H_D (m)	Observed period of swell T_D (sec)	Observed travel time of swell t_D (sec)	$\frac{H_D}{H_F}$	$\frac{T_D}{T_F}$	$\frac{t_D}{T_F}$	$\frac{D}{gT_F^2}$	Reference	Legend used in fig. 12	Manner of measurement[a]
1	18.5	835	6.48×10^{4}	2,320	6.8	7.9	1.4	11.5	2.70×10^{5}	0.21	1.46	3.42×10^{4}	3.79×10^{3}	------	Moroccan	a
2	14.4	1,110	1.06×10^{5}	1,480	4.8	8.1	2.6	17.0	1.80×10^{5}	.54	2.10	2.22×10^{4}	2.30×10^{3}	------	do	a
3	18.0	1,390	8.65×10^{4}	1,950	6.9	8.7	2.0	17.0	2.09×10^{5}	.29	1.95	2.40×10^{4}	2.63×10^{3}	------	do	a
4	13.9	1.300	2.27×10^{5}	1,110	4.9	10.5	2.7	11.2	1.51×10^{5}	.55	1.07	1.44×10^{4}	1.03×10^{3}	------	Berkeley	a
5	13.9	2,225	----------	1,480	5.1	12.2	3.0	9.1	1.95×10^{5}	.59	.75	1.60×10^{4}	1.02×10^{3}	------	do	a
6	9.8	2,225	2.43×10^{5}	185	2.5	9.0	2.1	9.5	2.88×10^{4}	.84	1.06	3.20×10^{3}	2.33×10^{2}	------	do	a
7	20.1	930	1.04×10^{5}	1,110	8.8	9.9	------	------	1.13×10^{5}	------	------	1.14×10^{4}	1.16×10^{3}	------	Pendeen	a
8	22.7	740	6.48×10^{4}	1,480	9.2	8.8	------	------	1.68×10^{5}	------	------	1.91×10^{4}	1.95×10^{3}	------	do	a

[a] See footnote of table I.

Contribution No. 304

NOTE ON THE CORRECTION OF REVERSING THERMOMETERS[1]

By

H. U. SVERDRUP

Scripps Institution of Oceanography, University of California
La Jolla, California

Corrections have to be applied to the readings of protected and unprotected reversing thermometers because they are read at a temperature that differs from that at the time of reversal. In deriving these corrections it is generally assumed that Feruglio's (1912) equation [(5) below] is exact. It is shown here that Feruglio's equation is not quite exact, but a close approximation. From this equation practical formulae, equations (6) and (8) below, can be derived very simply without further sacrifice of accuracy.

PROTECTED THERMOMETERS

Notations.

T_w : true water temperature at reversal.
T : reading of reversing thermometer.
I : index correction of thermometer.
$T' = T + I$: reading of reversing thermometer corrected for index error.
$\Delta T = T_w - T'$: correction to be applied with proper sign to reading in order to obtain true water temperature ($T_w = T' + \Delta T$).
$v_\circ$: volume of mercury below scale division "0 degree," expressed in °C.
$v_w = v_\circ + T_w$: volume of mercury at true water temperature.
$v_t = v_\circ + T'$: volume of mercury at reading.
t : temperature of auxiliary thermometer, that is, temperature of main thermometer at reading.
$1/K$: coefficient of thermal expansion of system glass-mercury expressed in unites $^\circ\mathrm{C}^{-1}$. For Jena glass 59^{III}, $K = 6100$, and for Jena glass 16^{III}, $K = 6300$.

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The change in volume of the torn-off column of mercury is

$$dv = \frac{1}{K}\,v dt\,. \tag{1}$$

Therefore, assuming K to be constant in the temperature range T_w to t:

$$\int_{T_w}^{t}\frac{dv}{v} = \frac{1}{K}\int_{T_w}^{t} dt\,, \tag{2}$$

or

$$ln\,\frac{v_t}{v_w} = \frac{1}{K}\,(t - T_w) = -\,(T_w - t)\,\frac{1}{K}\,. \tag{3}$$

Since

$$v_t = v_\circ + T' = v_\circ + T_w - \Delta T\,,$$

$$v_w = v_\circ + T_w\,,$$

it follows

$$ln\,\frac{v_t}{v_w} = ln\left(1 - \frac{\Delta T}{v_\circ + T_w}\right) = -\,\frac{T_w - t}{K}\,. \tag{4}$$

Expanding the logarithm in series and omitting terms, which, if retained, would result in a maximum error in ΔT of 0.002°, one obtains Feruglio's (1912) formula:

$$\Delta T = \frac{(T_w - t\,(v_\circ + T_w)}{K}\,. \tag{5}$$

Introducing $T_w = T' + \Delta T$ and omitting a term containing $(\Delta T)^2$:

$$\Delta T = \frac{(T' - t)\,(v_\circ + T')}{K - (T' - t) - (v_\circ + T')}\,. \tag{6}$$

This formula is nearly identical with the formulae by Schumacher (1923) and Hidaka (1932), but it is slightly more accurate. The advantage of the present derivation is that formula (4) is exact if K is a constant and that any desired degree of accuracy can be achieved by taking more terms into account when expanding the logarithm in (4) in series. This is in effect done by Hansen (1934).

In the above, the index correction has been applied before computing ΔT, but in practice this refinement is not necessary if the index correction is less than 0.1°. In (6) T' can be replaced by T, the reading of the reversing thermometer, and the index correction can be combined with ΔT to give the total correction. Furthermore, since the numerical value of the sum $(T' - t) + (v_\circ + T')$ generally is about 100, the denominator in (6) can be taken as 6000 or 6200 for Jena glass 59^{III} and 16^{III} respectively.

UNPROTECTED THERMOMETERS

Notations. As above, adding subscript u to reading and corrected values of unprotected thermometer. Thus $T_{w,u}$ represents the true value recorded by the unprotected thermometer at reversal and $\Delta T_u = T_{w,u} - T_u'$.

Equations (1) to (3) remain unaltered but (4) becomes

$$ln \frac{v_t}{v_w} = ln \left(1 - \frac{\Delta T_u}{v_0 + T_{w,u}}\right) = - \frac{T_w - t}{K}, \qquad (7)$$

which is exact if K is constant. Expanding the logarithm and introducing $T_{w,u} = T_u' + \Delta T_u$ leads to the close approximation:

$$\Delta T_u = \frac{(T_w - t)\,(v_0 + T_u')}{K - (T_w - t)}. \qquad (8)$$

Equation (8) is nearly identical with Schumacher's formula (1923).

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Contribution No. 305

nsactions, American Geophysical Union Volume 28, Number 3 June 1947

PERIOD INCREASE OF OCEAN SWELL

H. U. Sverdrup

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Abstract--It can be considered well established that the observed periods of ocean swell are longer than the observed periods of the waves in the generating area. More recently it has been demonstrated that a wave spectrum is always present and that observed periods refer to the periods of the highest waves in the spectrum, the waves of maximum energy. These are called the significant waves. Furthermore, Munk has shown that at least the forerunners of swell have the character of impulsively generated waves in deep water which advance as conservative waves.

Assuming that swell generally has these characteristics, it is shown that the air resistance which the swell encounters leads to a selective dissipation. The energy associated with the shorter period waves is dissipated more rapidly than that of the longer period waves, and consequently the energy maximum shifts toward longer periods, that is, the period of the significant waves increases. The effect is modified by following or opposing winds. Numerical examples are in satisfactory agreement with results from the semi-empirical graphs of Sverdrup and Munk.

The energy considerations indicate numerous new possibilities for the interpretation of records of swell, and it is hoped that these suggestions will further stimulate the effort to establish well located swell-recording stations and to develop instruments for rapid analysis of wave records that give complete information as to the wave spectrum.

Introduction

After decades of discussion, it is now generally agreed that the observed periods of swell m a distant source are longer than the periods of the waves in the source region, the gener- ig area. So far, no satisfactory explanation has been offered for this period increase. When ERDRUP and MUNK [see "References" at end of paper, 1946] established relationships which, the one hand, served forecasting purposes and, on the other hand, gave a framework into which erved values could be fitted, their approach was not intended as an examination of the processes ch explain the observed period increase.

Before attempting any explanation it is necessary to specify what is meant by "observed iods." Detailed records of waves in the generating area [EHRING, 1940] and of swell [MUNK, 7a] have demonstrated that not only the waves in the generating area are extremely compli- ed but swell is also complex, even though it may appear quite regular. In the case of swell s complexity has been brought out by the analysis of wave records obtained at Pendeen, Eng- d, by the British Admiralty Wave Research Group and at Cuttyhunk, Massachusetts, by the ods Hole Oceanographic Institution. These analyses demonstrate that during a 20- to 30-minute erval the swell is composed of waves of widely different periods.

In Figure 1, which shows an analysis of a record of swell at Pendeen, England [BARBER, SELL, DARBYSHIRE, and TUCKER, 1946], the wave periods are entered along the abscissa the ordinate gives an approximate measure of the heights of the waves and the frequency with ch waves of different periods occur. Thus, in the example, the predominant waves had periods ween 13 and 15 seconds, but waves of periods ranging from 10 to 24 seconds were also record- Under such conditions an observer would visually recognize only the high waves of periods 13 5 seconds because these would mask all lower waves of shorter or longer periods. In order to racterize the higher waves the term "significant waves" has been introduced [SVERDRUP and NK, 1946] to refer to "waves having the average height and period of the highest one-third of the es."

Experience gained so far indicates that the concept of significant waves is very useful and

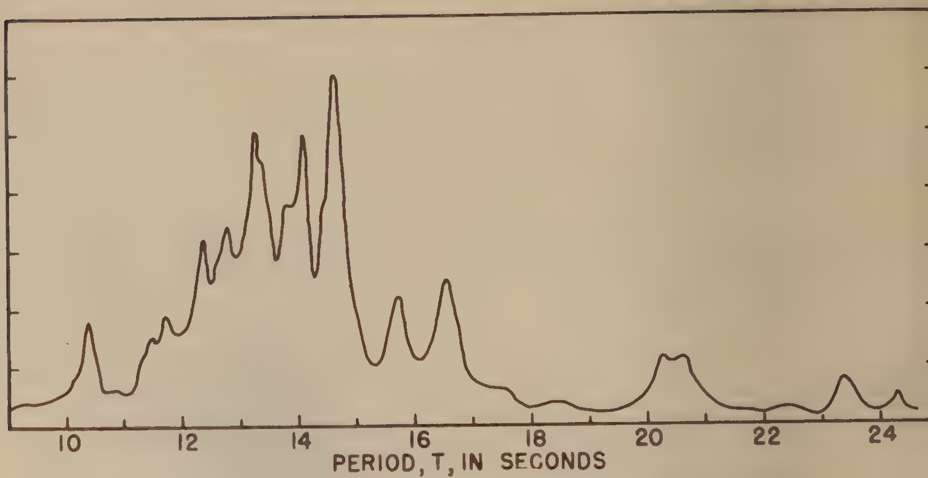

Fig. 1--Spectrogram of ocean swell recorded at Pendeen, England

that independent observers arrive at nearly the same values for wave height and wave period i
during a time interval of 10 to 20 minutes, they record only the highest two or three waves in
every group. Since these are most readily recognized, it seems probable that earlier observa-
tions all refer to the higher waves present and that, in general, "observed waves" represent a
proximately the significant waves as defined above. Therefore, the empirical evidence as to pe
increase is best stated by saying that the period of the *significant waves* increases. This incre
is quite unrelated to the period increase of *individual waves* which has been discussed by MUN
[1947a].

The realization of the general existence of a period *spectrum* with maximum wave heights
(significant waves) somewhere in the spectrum places the problem of period increase in an entirely different light. An increase in the period of the significant waves implies now that with
creasing travel time the region of maximum wave height shifts toward longer wave periods, th
is, towards lower frequencies. The occurrence of a shift of this nature indicates that the adva
ing swell is subject to a selective attenuation by which the energy of the higher frequencies (th
shorter periods) is more rapidly dissipated than that of the lower frequencies. It will be show
here, first, that a period spectrum can be expected to be present in the generating area if the
waves can be considered as being impulsively generated and, second, that the air resistance wh
the advancing swell meets is selective and must lead to an increase of period of the significant
waves.

Kinematics of surface waves in deep water

Conservative waves--Wave motion is called conservative in a region AB if in a time inter
$t >> T$, no crests are generated or destroyed (ROSSBY, 1945; MUNK, 1947b). This condition c
be written

$$\partial(1/L)/\partial t + \partial(1/T)/\partial x = 0 \ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

where L is wave length and T is wave period. The wave velocity C, which will be referred to a
phase velocity, is by definition equal to L/T, and in deep water, according to the classical theo

$$C = (g/2\pi)T \qquad L = (g/2\pi)T^2 \ldots\ldots\ldots\ldots\ldots\ldots$$

By means of (2), equation (1) takes the form

$$\partial T/\partial t + (C/2)\partial T/\partial x = 0 \ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

Using the symbol d/dt for the time rate of change when traveling with velocity C/2, it follows

$$dT/dt = \partial T/\partial t + (C/2)\partial T/\partial x = 0 \ldots\ldots\ldots\ldots\ldots\ldots$$

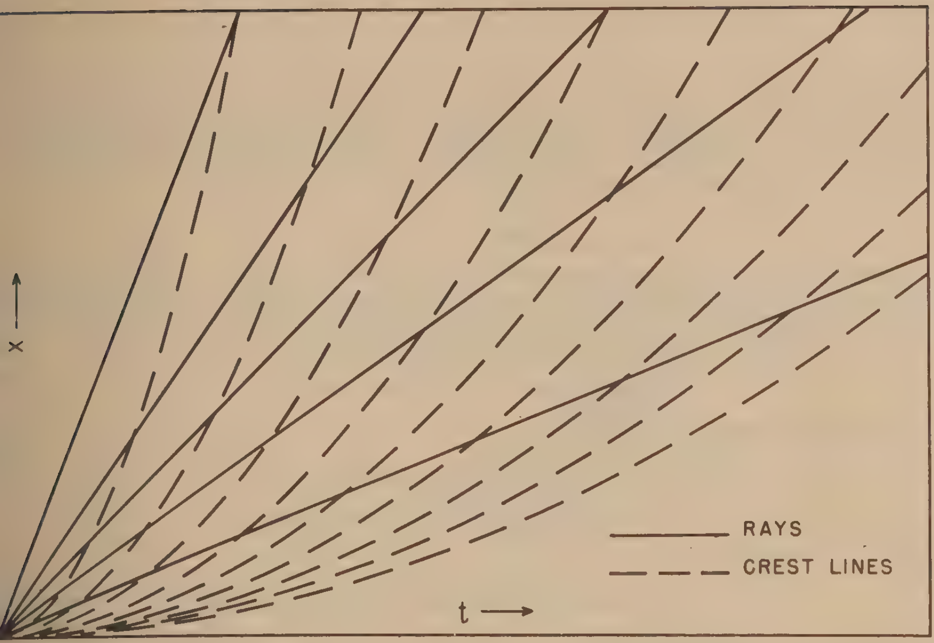

Fig. 2--Rays and crest-lines of surface waves in deep water, represented in a t-x diagram

he velocity C/2 represents the group velocity of surface waves in deep water. Equations (3) and) are also valid if a general symbol for group velocity is introduced.

Impulsively generated waves--An initial displacement of the free surface which at t = 0 is onfined to the immediate neighborhood of x = 0 will produce a wave train which, at a distance x 1at is small compared to gt^2, is characterized by a slow decrease in the time interval between assages of successive wave crests. In the Cauchy-Poisson wave problem [LAMB, 1932, pp. 84-489] this interval, T, is

$$T = (4\pi/g)(x/t) \quad \ldots\ldots\ldots\ldots \quad (5)$$

here g is the acceleration of gravity. This value of T can be considered generally valid when ealing with centered impulsively generated conservative waves in deep water. It represents the bserved period of the passing waves.

According to (5), lines of constant period (T = constant) are straight lines through the origin 1 a diagram with t and x as coordinates (see Fig. 2). These lines are called rays. The path of n observer who travels with a constant group velocity,

$$C/2 = (g/4\pi)T = x/t = \text{constant}$$

s represented by a ray in the t-x diagram. Such an observer will record that wave period and ave length in his neighborhood remain constant. He will also record that he is continuously being overtaken by individual waves which travel at twice his own speed.

Let the notation D/Dt indicate the time rate of change of an individual wave. Then, using (4) nd (5)

$$DT/Dt = \partial T/\partial t + C(\partial T/\partial x) = - \partial T/\partial t = T/t \quad \ldots\ldots\ldots\ldots \quad (6)$$

y integration,

$$T/T_n = t/t_n \quad \ldots\ldots\ldots\ldots \quad (7)$$

where the T_n indicates the period at the time t_n. By means of (5) one obtains

$$t = t_n \sqrt{x/x_n} \quad \text{(8}$$

In the t-x plane, equations (7) and (8) define a family of curves through points t_n, x_n at which T has the value T_n. Each of these curves represents the path of an observer who travels phase velocity $C = 2x/t$. Such an observer starting out on a crest will always remain on the sam crest and the curves are therefore called crest lines. They are also shown in Figure 2, from which it is seen that along the crest line the period increases continuously.

Energy considerations

General equations--Assume that no wave energy is added or dissipated locally. On this assumption the local time change in wave energy E must equal the difference between the amounts of wave energy that enter and leave a volume. Since wave energy advances with group velocity follows that [ROSSBY, 1945; SVERDRUP and MUNK, 1946]

$$\partial E/\partial t + \partial(CE/2)/\partial x = 0 \quad \text{(}$$

Using the relationships

$$\partial E/\partial t = dE/dt - (C/2)\partial E/\partial x \quad \text{(1}$$

$$\partial(CE/2)/\partial x = (E/2)\partial C/\partial x + (C/2)\partial E/\partial x$$

and, from (2), (3), and (6),

$$(1/2)\partial C/\partial x = -(1/C)\partial C/\partial t = -(1/T)\partial T/\partial t = 1/t$$

one obtains by substitutions into (9)

$$(1/E)dE/dt = -1/t \quad \text{(1}$$

In equations (4) and (9) a general symbol V could have been introduced for the group velocit instead of C/2, and one would have obtained the general equation

$$(1/E)dE/dt + \partial V/\partial x = 0 \quad \text{(1}$$

of which (11) is a special form applicable to surface waves in deep water.

The use of equation (10) implies that we examine the change in energy which will be record by an observer who travels with group velocity. By integrating (11)

$$E/E_1 = t_1/t = x_1/x \quad \text{(13}$$

For deep-water waves of small steepness, E is proportional to the square of the wave height H. Therefore

$$H/H_1 = \sqrt{t_1/t} = \sqrt{x_1/x} \quad \text{(13}$$

Thus, along any given ray, the wave height is proportional to the square root of the ratio betwee travel times or travel distance, but generally the factor of proportionality varies from ray to ra

Application to wave spectrum--Assume that numerous wave trains are generated by a seri of disturbances at $x = 0$, starting at $t = 0$ and continuing for a long time. Assume, furthermore, that waves from these disturbances arrive at $x = x_1$, ($x_1 << gt^2$), with heights depending upon th period as indicated in Figure 3, that is, that the wave heights are small for short periods, incre to a maximum at an intermediate period, and decrease more slowly at longer periods. This is equivalent to assuming that at $x = x_1$ and at a time $t = t_1$, where t_1 is the travel time of shortes waves from $x = 0$ to $x = x_1$

$$\left.\begin{array}{c} H = H(T) \\ dH/dT = 0 \text{ for } T = T_m \\ H \rightarrow 0 \text{ as } T \rightarrow 0, \text{ and } H \rightarrow 0 \text{ as } T \rightarrow \infty \end{array}\right\} \quad \text{(}$$

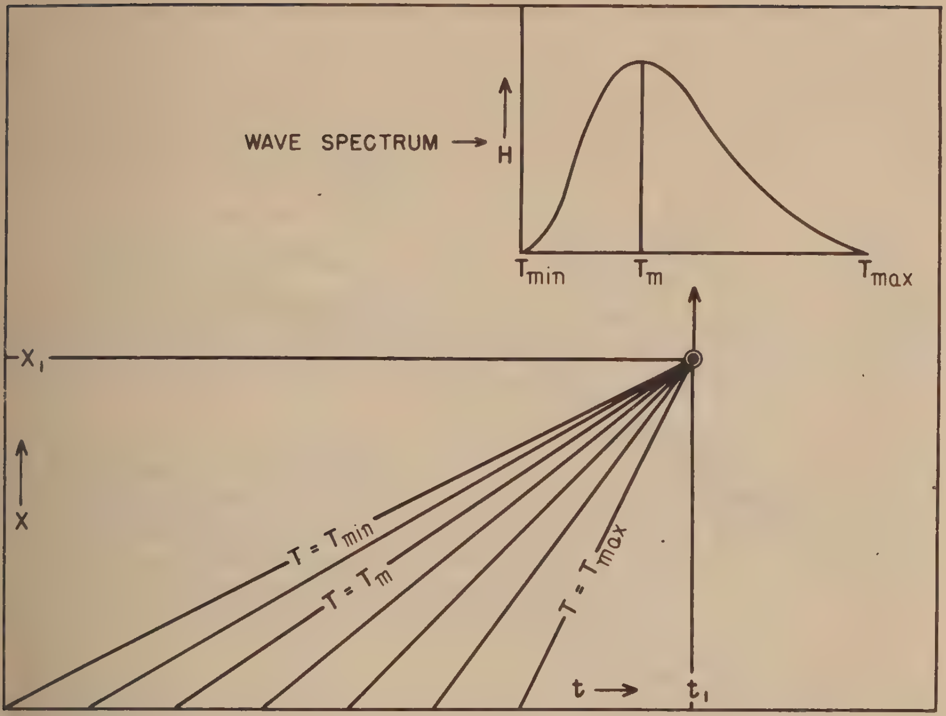

Fig. 3--Wave spectrum at $x = x_1$, $t = t_1$ as a result of numerous wave trains emitted from $x = 0$ in the time interval between $t = 0$ and $t = t_1$

These relationships between H and T represent approximately the average conditions that xist at the end of a fetch where waves raised by wind are present. At a given instant the wave attern must probably be considered as consisting of a limited number of distinct waves, but over time interval of one or more hours conditions of (14) may be approximately satisfied [EHRING, 940]. The waves can probably be considered as being impulsively generated, but they may not ave traveled the same distance before they arrived at the end of the fetch. Still, it is of interest examine the conclusions which on this basis can be drawn as to the character of the swell manating from the fetch and to compare these conclusions with empirical evidence.

The graph prepared by SVERDRUP and MUNK [1946] for forecasting swell appears to be fair- consistent with observations, and for present purposes of comparison is considered to repre- ent observational data. A comparison between the contents of this graph and the preceding theory eveals, however, the following discrepancies, as shown in Figure 4: (a) The computed decrease wave height is much smaller than observed; (b) the period of the highest waves remains con- ant, whereas observations indicate that this period increases; and (c) the travel time of the high- st swell is obtained from the constant group velocity of the highest waves at the end of fetch but much longer than indicated by the observations.

Effect of air resistance on waves traveling through regions of calm--The listed discrepancies n be eliminated to a great extent by taking into account the air resistance that must be encoun- red by swell traveling through regions of calm. The local loss of wave energy per unit time used by air resistance [SVERDRUP and MUNK, 1946, eq. 84] is

$$R_N = -s(\rho'/\rho)g(E/C) = -s(\rho'/\rho)(2\pi/T)E \quad \ldots\ldots\ldots\ldots\ldots \quad (15)$$

ere $s = 0.013$ and is the "sheltering coefficient," ρ' is the density of the air, and ρ the density the water. This term has to be added on the right-hand side of (9). Equation (11) then takes t form

$$(1/E)dE/dt = -1/t - s(\rho'/\rho)(2\pi/T) \quad \ldots\ldots\ldots\ldots\ldots \quad (16)$$

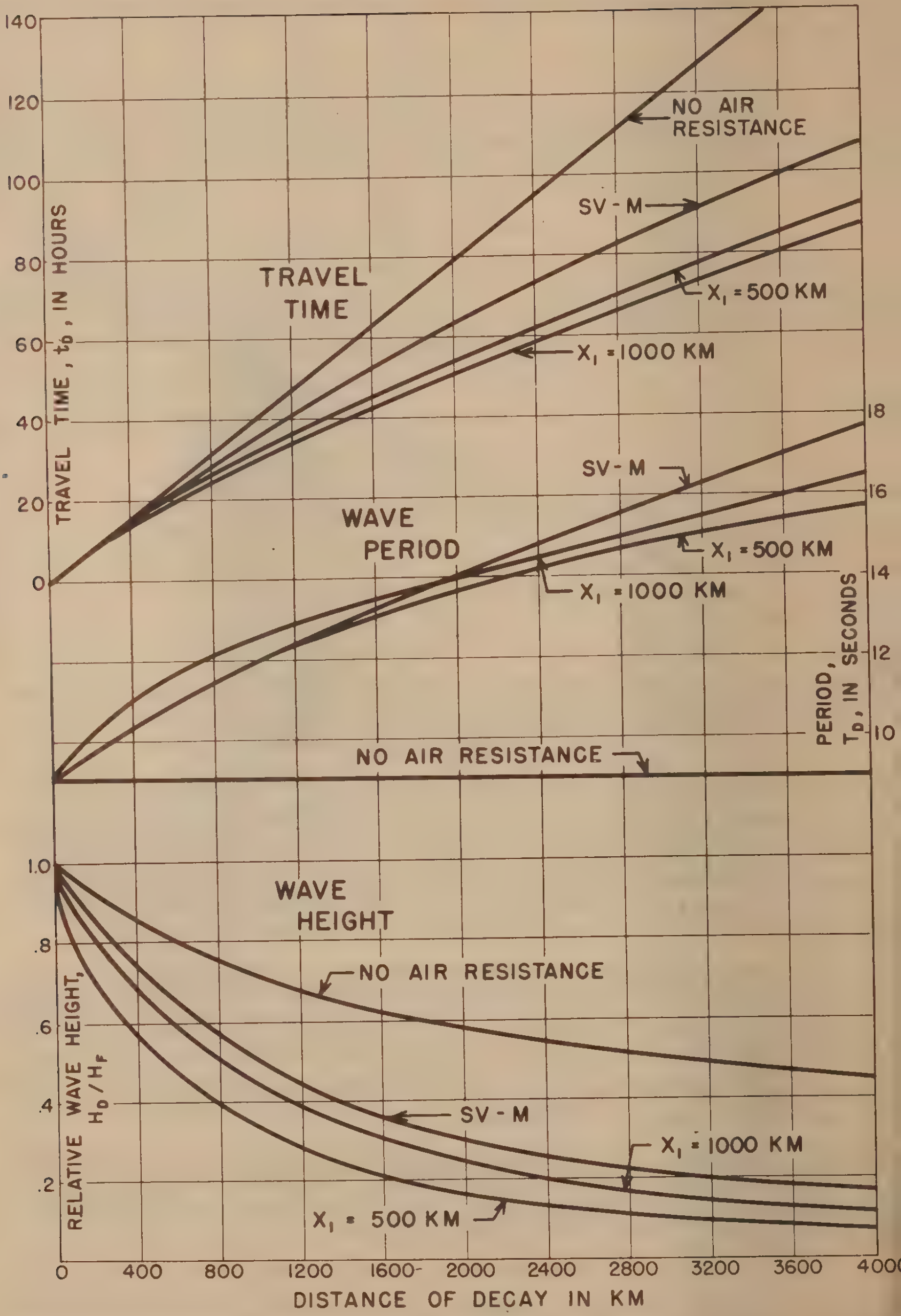

Fig. 4--Travel time, period, and relative height of significant waves as functions of distance of decay, according to the graph by Sverdrup and Munk (Sv - M) for T_F = 9 seconds, and according to Fig. 5 (x_1 = 1000 km) and Fig. 6 (x_1 = 500 km) emembering that dE/dt represents the total change in energy along a line of constant period, one btains by integration

$$\log_e (E/E_1) = \log_e (t_1/t) - s(\rho'/\rho) 2\pi (t - t_1)/T_1 \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (16)$$

r, using (5), taking into consideration that E is proportional to H^2

$$\log_e (H/H_1) = (1/2) \log_e (x_1/x) - s(\rho'/\rho)(4\pi^2/g)(x - x_1)/T_1^2 \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (17a)$$

$$= (1/2) \log_e (x_1/x) - (K/T_1^2)(x - x_1) \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (17b)$$

here $K = 6.37 \times 10^{-7}$ ($cm^{-1} sec^2$).

It follows from (17) that over a given distance, $x - x_1$, the decrease in height must be larger han according to (13b), and that the short-period waves decrease faster than the long-period ones. onsequently, the height maximum must shift toward the longer waves. The travel time which is btained from the group velocity of these longer waves is shorter than the travel time without air esistance. Thus, the modifications are all in the direction indicated by the observations.

It remains to be shown that (17) gives numerical results in approximate agreement with ob- ervations. Since the first term on the right-hand side of (17) depends upon the ratio x_1/x, where- s the last term depends upon the difference $x - x_1$, the rate at which H decreases for a given dis- nce $x - x_1$ depends upon the value of x_1. The larger x_1, the slower will be the decrease. We hall examine two cases, $x_1 = 10 \times 10^7$cm (1000 km) and $x_1 = 5 \times 10^7$cm (500 km). In each case e shall assume that at $x = x_1$ the wave height is at a maximum at T = 9 seconds. Taking x_1 as e length of the fetch and identifying the highest waves with the significant waves, we find from e graphs for generation of waves that in the first case a wind of 23 knots must have blown for 54 ours over a 1000-km (540-mile) fetch, that in the second case a wind of 35 knots has blown for 7 hours over a 500-km (270-mile) fetch.

The assumption that the waves at the end of the fetch can be considered as centered impul- ively generated waves, represents an over-simplification. Actually, the value of x_1 may differ r the different parts of the wave spectrum and may vary within the same part of the spectrum. aves for which x_1 is small will, according to (17), decrease rapidly in height and will soon dis- ppear from the spectrum of the swell. In (17) x_1 may therefore be interpreted as applicable to ose waves at the end of the fetch that have traveled the longest distance, and it is justified to t x_1 represent the length of the fetch. The distance $x - x_1$ represents the distance of decay.

Figures 5 and 6 show the assumed variation in wave height with wave period at the end of the tch, also the computed variations at different distances of decay, varying from 100 km to 6,000 m. The disappearance of the short-period waves and the shift of the maximum wave height ward longer periods is apparent in both cases. It is also evident that in records of swell the ng-period waves, whose significance was discussed by MUNK [1947a], appear prominently be- ause these waves decrease more slowly in height than the waves of shorter periods.

Figure 4 shows a comparison between computed values and those from Sverdrup and Munk's raph. The relative height of the swell, the period and the travel time are plotted against distance of ecay. For the computed values the curves refer to the highest waves, assuming that these can be onsidered the significant waves. The assumption of no air resistance is obviously in complete isagreement with the contents of the Sverdrup-Munk graph, but by taking air resistance into ac- ount both examples give an increase in period similar to that obtained from the graph. The ravel times, however, are about 15 per cent shorter and the decrease in wave height is faster, articularly with $x_1 = 500$ km. The overall agreement is better with $x_1 = 1000$ km. One could elect such values of x_1 and of $H = H(T)$ for $x = x_1$ that a close agreement with the results from e graphs could be achieved, except for the travel time which would be shorter, but there is no oint in doing so because there exists no observational basis for selecting any particular function $= H(T)$, nor any basis for assigning a particular value to x_1.

The fair numerical agreement obtained indicates that the processes considered here are esponsible for some of the characteristic properties of swell. If this is true one should further- ore expect that: (1) Swell from a short fetch decays more rapidly than swell for a long fetch;) the period increase of the main swell depends upon the character of the wave spectrum at the nd of the fetch which, in turn, may depend upon the length of the fetch and upon the wind velocity;) the travel time of the main swell is probably about 15 per cent shorter than according to the verdrup-Munk graph.

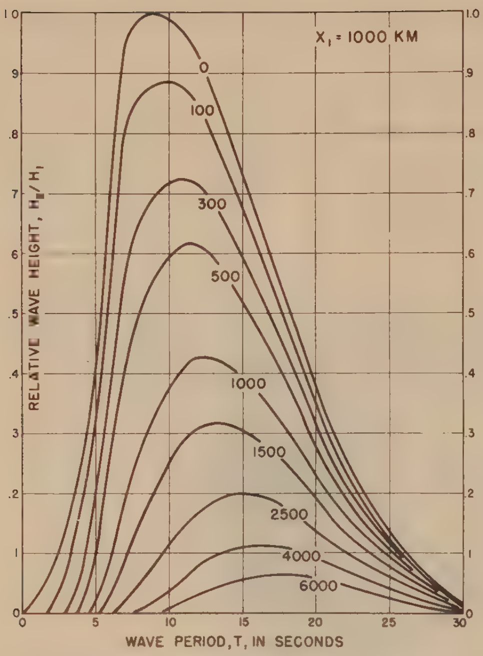

Fig. 5--Assumed variation of wave height with period at the end of a 1000-km fetch (curve marked 0) and computed variations at distances of decay ranging from 100 to 6,000 km

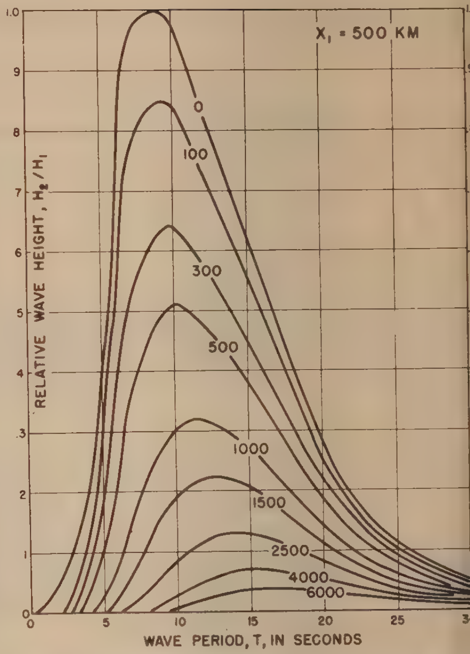

Fig. 6--Assumed variation of wave height with period at the end of a 500-km fetch (curve marked 0) and computed variations at distances of decay ranging from 100 to 6,000 km

A few observations do indicate that the travel time is shorter than obtained from the graph, but many more observations are needed for further examination of this and the other features.

Effect of viscosity--In order to consider the effect of viscosity, it is necessary to add the term [LAMB, 1932, p. 624]

$$- 4\nu\,(2\pi/T)^4\,E/g^2$$

to the right-hand side of (9). Here, ν is the kinematic viscosity of water which for sea water of temperature 15° and salinity 35 $^{o}/oo$ has the value 0.012 (cm^2/sec). Introducing this term and retaining the term for air resistance gives

$$\log_e (H/H_1) = (1/2)\log_e (x/x_1) - (\rho'/\rho)(s/g)(2\pi/T)^2\,[1 + (\rho/\rho')(4\nu/sg^2)(2\pi/T)^3]\,(x - x_1)$$

With the above value of ν one obtains for the last term in the parenthesis

T =	5	10	15	20 sec
Term =	6.2×10^{-3}	8.2×10^{-4}	2.3×10^{-4}	9.8×10^{-5}.

Thus, the effect of ordinary viscosity is negligible, and swell traveling through regions of calm i not influenced by viscosity. With a weak wind even the accompanying eddy viscosity would have effect and it may therefore be concluded that viscosity need not be considered when dealing with the decay of swell.

Effect of weak following and opposing winds--The effects of weak following and opposing win (C > U) can be treated by adding to the right-hand side of (9) the complete term representing energy transfer. For a following wind this term is

$$E(\rho'/\rho)(2\pi/T)\,[2\gamma^2 (U/C)^2 - s(C - U)^2/C^2] \quad \ldots\ldots\ldots\ldots\ldots (1$$

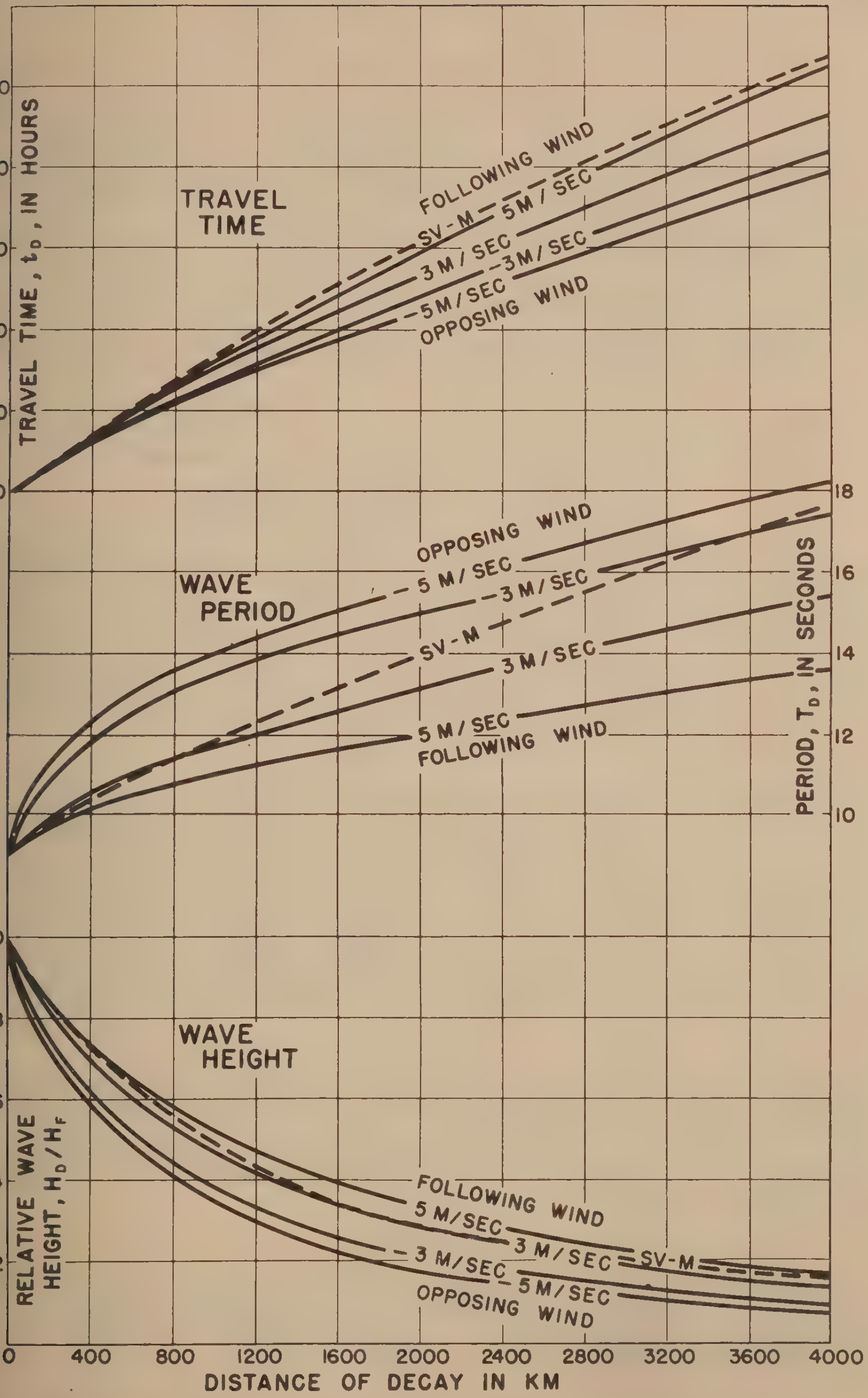

Fig. 7--Travel time, period, and relative height of significant waves as functions of distance of decay according to the graph by Sverdrup and Munk (Sv - M) for T_F = 9 seconds, and according to computations, assuming the initial variation of height with period shown in Fig. 5 for x_1 = 1000 km (curve marked 0) and following or opposing winds of 3 and 5 m/sec where U is the wind velocity and γ^2 the resistance coefficient, and for an opposing wind it is

$$E(\rho'/\rho)(2\pi/T)\,[-\,2\gamma^2(U/C)^2 - s(C + U)^2/C^2] \qquad (1$$

In both cases it is assumed that $C > U$, but this is no serious restriction because for $C < U$ wav generation takes place. For moderate and strong winds the generation becomes an important feature and must be treated separately, but here we are interested in the effect of weak winds.

For winds above about 6 m/sec the resistance coefficient equals 2.6×10^{-3}, but for weaker winds its value is only about 0.9×10^{-3}. The sheltering coefficient s equals 1.3×10^{-2} as befor It can therefore readily be ascertained that with weak winds of velocities less than about 6 m/se only the last term in (18) or (19) needs to be considered.

For following and opposing winds less than 6 m/sec the decay of swell is therefore obtaine from the equation

$$\log_e (H_2/H_1) = (1/2) \log_e (x_1/x_2) - (K/T^2)\,[(C \mp U)^2/C^2]\,(x_2 - x_1)$$

where $-$ is for following winds and $+$ for opposing, and where, as previously,

$$K = s(\rho'/\rho)(4\pi^2/g) = 6.37 \times 10^{-7}\ (\mathrm{cm}^{-1}\ \mathrm{sec}^2)$$

Figure 7 corresponds to Figure 4 and shows the relative wave height, the apparent period i crease, and the travel time for following and opposing winds of 3 and 5 m/sec, corresponding to the initial distribution of wave energy shown in Figure 6 and x_1 = 1000 km. A weak following wi acting over long distances, leads to a change in height of swell that is more consistent with the Sverdrup-Munk curves. The increase in period is still in fair agreement with the Sverdrup-Mu results but the travel time is shorter than theirs. Since the meager evidence used to substantia the graphs is based upon observations in middle latitudes with prevailing westerly winds, it is possible that an effect of prevailing following winds is incorporated in the graphs. It must be er phasized again, however, that one cannot give great weight to agreements between numerical re sults because there exist too many possibilities for adjusting them.

Conclusions--The main conclusion is that no striking inconsistencies exist between the em pirical evidence and the results of the present analysis which is based on the assumptions that wind raises impulsively generated waves and that beyond the generating area these advance as conservative waves that meet an air resistance. Furthermore, the analysis suggests that the swell may be characterized by a number of features which so far have not been recognized because no records have been available which could reveal their existence. It has already been demonstrated by MUNK [1947b] that by using conclusions based on the kinematics of surface waves, records of swell give information as to the distance to and speed of travel of the storm which the waves were generated. The energy considerations introduced here have opened a num ber of new possibilities for further interpretation of the records of swell. The present discussi deals only with propagation in one dimension but can be expanded to include problems in two dimensions.

It is hoped that these suggestions will further stimulate the efforts to establish well locate swell-recording stations. It would be of particular interest to have two stations in the path of frequent swell and 500 to 2000 miles apart, in order to determine the accurate value of the shelt ing coefficient, examine the following and opposing winds, and to study the possible significance of the length of the fetch and the wind velocity upon the wave spectrum and the rate of decay. F these purposes it is very desirable to develop instruments for rapid analysis of wave records w give complete information about the wave spectrum.

Acknowledgments

The preceding attempt at dealing with swell as impulsively generated conservative waves w stimulated by a series of lectures on wave theory by Carl Eckart, Director of the Marine Physical Laboratory, University of California. The ideas in this paper have been clarified duri discussions with my collaborators, R. S. Arthur and W. H. Munk.

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Scripps Institution of Oceanography,
University of California,
La Jolla, California

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TRACKING STORMS BY FORERUNNERS OF SWELL

By Walter H. Munk

Scripps Institution of Oceanography,[1] University of California, La Jolla

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ABSTRACT

Long, low waves preceding the arrival of the visible swell from a storm have been recorded off Pendeen, England, and Woods Hole, Massachusetts, by means of new instruments for the measurement and analysis of ocean waves. These forerunners provide storm warnings of practical value. Expressions giving the forerunner's distance from the storm system and its travel time as functions of recorded period and rate of change of period are derived from very general assumptions. The expressions are suitable for simple graphical representation. The application of the method to tracking storms across the ocean is illustrated by means of a few actual examples, and the computed storm tracks are shown to be in good agreement with the information contained on weather maps. Certain features of the wave records may eventually make it possible to compute not only the location but also the size, intensity, and general character of the storm.

Introduction

The use of swell as a sea-borne storm warning is
ite natural and has been recognized by seafaring
en since ancient times. In the early days of weather
ecasting in New Zealand, particular attention was
id to observations of swell. However, the interpreta-
n of swell appears to have been intuitive, based upon
perience gained in a lifetime at sea.

Here it has been attempted to develop a *quantitative*
thod for using wave observations to track storms
sea. The method depends on the use of special
truments for recording waves and on the interpreta-
n of the records in the light of hydrodynamics.

Another quantitative method, which differs entirely
m the one to be described here, was suggested by
relationships established for forecasting sea and
ell from weather maps (Sverdrup and Munk, 1947,
28). These relationships contain a quantitative
mulation of the common experience that relatively
h waves of short period come from a near-by storm,
ile low waves of long period come from a distant
rm. However, when these relationships are applied
a reverse manner, that is, in the computation of
rm properties from wave observations, the problem
no longer completely determinate. A number of
er inherent difficulties further limit the use of this
thod. Even with these limitations the method has
nd practical application.

The limitations can be overcome in part by dealing
h the low, long, invisible forerunners of the swell,
her than with the swell ordinarily observed. This
kes it impossible to apply simple, visual methods of observation, but the advantages involved appear to justify the use of special instrumental techniques. In the first place, the forerunners travel considerably faster than the visible swell, as the speed of waves in deep water is proportional to their period. On the basis of instrumental observations now available (Deacon, 1946), the period of the forerunners may reach values up to 30 sec, in contrast with the average swell period of about 10 sec. The corresponding speeds with which the disturbance created by a storm is effectively propagated by wave motion (group velocity) are of the order of 1100 nautical miles per day for the forerunners, in contrast with 400 nautical miles per day for the swell. In the case of a fairly distant storm, information carried by the visible swell therefore pertains to wind conditions which have existed a number of days before the swell is observed. In the case of a fast-moving storm system, the visible swell may give little or no advance warning. The speed of the forerunners, on the other hand, although slow compared with the speed of microseisms, radio waves, and other phenomena providing auxiliary weather data, may be sufficiently rapid to permit practical use of the information carried by the forerunners.

The other advantage in dealing with the forerunners rather than the visible swell is that the forerunners seem to have the characteristics of *conservative* waves, that is, waves whose crests maintain their identity over great distances. The crests of ordinary swell maintain their identity over much shorter distances. Although the difference is largely one of degree, it is important because the treatment of visible swell must depart from methods of classical hydrodynamics and take into account the statistical[2] nature of the

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ied out for the Hydrographic Office, the Office of Naval
earch, and the Bureau of Ships of the Navy Department
er contract with the University of California.

[2] C.-G. Rossby (verbal communication) has suggested that visible swell may be treated from a point of view closely akin to that of statistical mechanics.

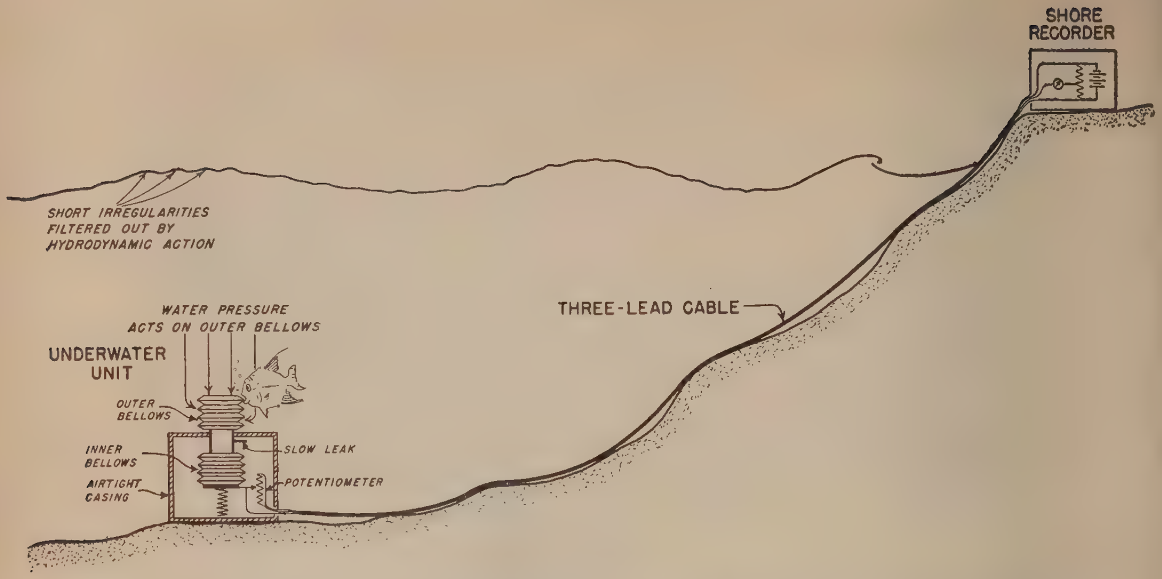

FIG. 1. Recording mechanism. The pressure fluctuation at the sea bottom is due to surface waves; it is picked up by the underwater unit and recorded on shore.

problem (Sverdrup and Munk, 1947, p. 12). The height and period of the visible swell do not suffice to determine uniquely the principal unknowns, travel time and storm distance; additional assumptions must be introduced, such as a relationship between storm intensity and storm size. The problem dealing with the conservative forerunners is much simpler. Travel time and storm distance can be uniquely determined without further assumptions. Furthermore, it is possible to carry out a purely kinematic analysis whereby the need for measuring wave height is eliminated and only a knowledge of wave period is required. In a determination of the deep-water wave height it is necessary to take into account, by means of specially constructed 'refraction diagrams' (Munk and Traylor, 1947), the effect of bottom topography and of the configuration of the coastlines. The response characteristics of the instruments also enter as an important factor. Wave periods, on the other hand, are relatively easy to ascertain from wave records and are not subject to the complex changes in wave pattern that occur as waves come into shallow water.

2. Instrumentation

The development of wave-recording instruments has been carried out simultaneously in Great Britain and the United States. An early model developed by the Mine Design Department, British Admiralty, has been in operation at Pendeen, near Lands End, England, for over two years (Deacon, 1946). Records taken by this instrument have been kindly placed at our disposal by the Oceanographic Research Group, Admiralty Research Laboratory, Teddington, England, and form the basis for the examples given in thi
report.

In the United States the development of wave ir
struments is chiefly due to M. Ewing of the Wood
Hole Oceanographic Institution. In the early model
the recording apparatus was contained directly in th
underwater unit. Later units recording on shore wer
installed near Cuttyhunk, Massachusetts, and at th
island of Bermuda.[3] A number of models have bee
developed at the College of Engineering, Universit
of California,[4] and some of these will be used in th
installation at the Scripps Institution.

Although the various instruments differ in man
important aspects, the following principles are con
mon to all and should be understood for a prope
interpretation of the final records. Surface waves ir
duce pressure fluctuations in the entire column
water between the surface and the sea bottom (fig. 1
For any given depth of water and wave height, th
amplitude of these fluctuations depends on the wav
period in such a manner that waves of very sho
period are virtually eliminated. The underwater un
measures the fluctuating pressure at the sea botton
A 'slow leak' in the underwater unit eliminates th
effect of tides and other very long waves. The pressu
fluctuations are converted into electrical modulation
which are transmitted through a cable to a sho
recorder. Finally the records are subjected to a ha

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[3] A. A. Klebba, "A summary of shore recording wavemete
preliminary report," Woods Hole Oceanographic Institutio
1945.

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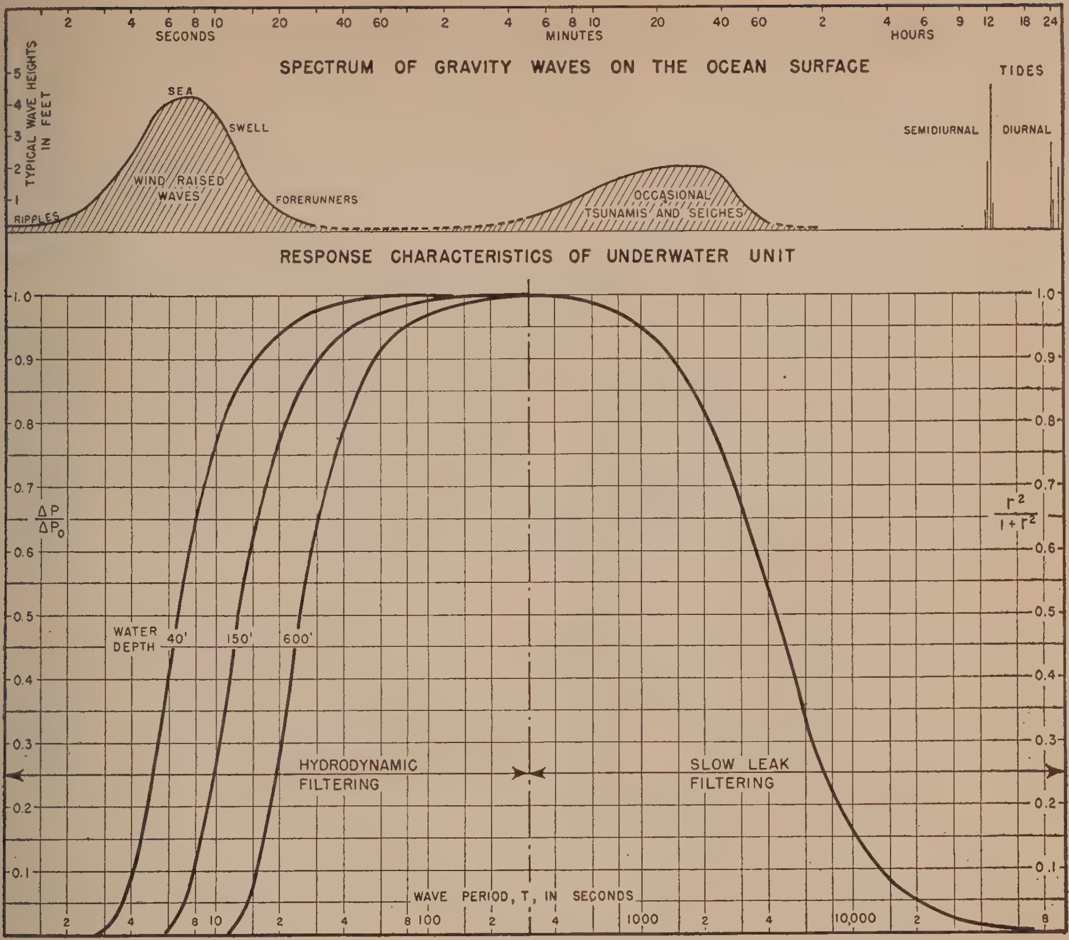

Fig. 2. Upper portion, a typical distribution of energy among various types of ocean waves, ranging from wind ripples having a eriod of one second to tides having periods of 12 and 24 hours; lower portion, the over-all response characteristics of the underwater nstruments. Both graphs are drawn to the same period scale.

monic analysis by a special instrument. The natural wave spectrum is therefore modified in three stages: (a) waves of short period are removed by hydrodynamic filtering; (b) waves of very long period are removed by the slow leak in the underwater unit; (c) the remaining record is broken down further by harmonic analysis.

Hydrodynamic filtering.—Owing to their low amplitude, the forerunners must be extracted from the complex pattern of the sea surface by means of special techniques. One technique uses the ocean itself as a highly effective low-pass filter. The response characteristics of this filter can be expressed by the ratio $\Delta P/\Delta P_0$ of the amplitude of the pressure fluctuation at the bottom to that just beneath the surface. Let h designate the water depth, L the wave length, T the wave period, and g the acceleration due to gravity. The depth L can be eliminated between the equation

$$\frac{\Delta P}{\Delta P_0} = \frac{1}{\cosh\,(2\pi h/L)}$$

and the well known relationship

$$\left(\frac{2\pi}{T}\right)^2 = \frac{2\pi g}{L} \tanh \frac{2\pi h}{L},$$

so that the hydrodynamic filtering effect $\Delta P/\Delta P_0$ can be computed as a function of depth and wave period.[5]

The left sides of the curves in the lower part of fig. 2 have been computed in this manner for three selected depths. Thus, at depths of 40, 150, and 600 feet, waves of periods less than 4, 8, and 15 sec respectively are practically eliminated. The underwater unit of the Woods Hole Oceanographic Institution is situated at an average depth of 80 feet, the unit of the British Admiralty Research Laboratory (Barber, Ursell, Darbyshire and Tucker, 1946) at an average depth of 120 feet. Comparison of the upper and lower parts of fig. 2 shows that at these depths the visible swell is not effectively reduced; therefore neither instrument is particularly suited for the recording of the forerunners, as would be an instrument at 600 feet. The proposed wave station of the Scripps Institution of Oceanography provides for three underwater units at depths of 40, 150, and 600 feet. According to fig. 2, the deep unit will be out of reach of the visible swell and can be designed to record the low forerunners with great sensitivity. Fortunately a submarine canyon enables the deep instrument to be placed only 3000 feet from the end of a pier. In most localities it will be cheaper, though hardly more effective, to suppress the short-period waves instrumentally.

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[5] W. H. Munk, "Measurement of waves from pressure fluctuations at ocean bottom," Scripps Institution Wave Project Report No. 5, 1944.

The underwater unit.—Fig. 1 gives a schematic view of one type of underwater unit and serves to illustrate the desired characteristics. The pressure P_w is transmitted through an outer bellows into a second bellows inside the instrument casing. Thus the pressure of the air inside the two bellows always equals the pressure in the water outside. The air inside the bellows can pass through a slow leak into the instrument casing, so that the *average* pressure inside the casing equals the average pressure in the water, that is, the hydrostatic pressure P_h. The leak is so slow that the pressure inside the instrument does not change appreciably during one wave period.

The total displacement of the inner bellows depends on the *difference* in pressure between the inside and the outside of the bellows and therefore measures the deviations of pressure from the hydrostatic mean. These deviations have an amplitude ΔP.

For waves of very long periods the fluctuation of air pressure in the instrument casing cannot be neglected. Indeed waves of tidal period are almost completely eliminated from the record, as the slow leak is able to compensate for the gradual rise and fall of sea level during a tidal cycle. In the general case the amplitude response of the instrument is proportional to $r^2/(1+r^2)$, where $r = T_r/T$; T_r is the 'resonance' period, which depends on the size of the slow leak, the air volume of the instrument, and the water depth. In fig. 2, T_r has been assumed to equal about one hour. Owing to the combined effect of hydrodynamic filtering and the slow leak, waves of short and very long period are effectively eliminated. Maximum sensitivity is achieved in the desired range by a proper choice of depth for the underwater unit and of size for the 'slow leak.'

Frequency analyzer.—The following description refers to the analyzer developed at the Admiralty Research Laboratory (Barber, Ursell, Darbyshire and Tucker, 1946). The pressure deviations are recorded photographically on shore. The finished record is half black and half white, and the deflection of the black-white boundary is proportional to the pressure deviation. Each record covers an interval of about 20 minutes. The record is placed in the analyzer by wrapping it around the circumference of a heavy wheel, which is rotated and permitted to slow down by friction. A narrow band of light is thrown on the record, and the record is scanned photoelectrically. The current fluctuation in the photoelectric-cell circuit follows the fluctuation on the record. The current output is amplified and fed into a vibration galvanometer with a sharp resonance characteristic of about 100 cycles, and the output of the galvanometer is mechanically plotted against the angular velocity of the wheel. A set of period analyses is shown in fig. 6.

Wave direction.—Two methods for measuring wave direction are being studied. One depends on the measurement of the time interval between the passage of a wave crest over two underwater units placed equally distant from shore. The other method depends on the use of a Rayleigh disk. The development of a reliable method for measuring wave direction is an essential requirement in making use of wave records for tracking storms.

3. Kinematics of conservative waves

Certain properties peculiar to conservative wave motion are derived in this section; these properties form the basis of the method for tracking storms by forerunners of swell. Wave length is defined as the horizontal distance between two adjacent wave crests, wave period as the time interval between the appearance of two successive crests at a fixed spot. It should be noted that these definitions refer not to the underlying regular wave trains of a Fourier spectrum but to the physical deformations of the sea surface (Munk, 1947). The following analysis deals with a train of waves in which the wave length L and the wave period T are slowly varying functions of time and distance.

The wave length L of a wave traveling with (phase) velocity C along the positive x-axis changes at the rate[6]

$$\frac{DL}{Dt} = \frac{\partial L}{\partial t} + \frac{\partial L}{\partial x} C. \qquad (1)$$

This change can also be found from the rate at which the wave 'stretches' due to the difference in speed of two adjoining crests:

$$\frac{DL}{Dt} = \frac{\partial C}{\partial x} L = \frac{dC}{dL}\frac{\partial L}{\partial x} L. \qquad (2)$$

The latter substitution is possible in a dispersive medium where C is a function of L only. Combining (1) and (2) gives

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[6] The notation D/Dt denotes the rate of change with respect to an observer moving with a *fixed wave*, in analogy with a convention introduced by Stokes according to which D/Dt denotes the 'material' derivative, that is, the rate of change with respect to an observer moving with a *fixed particle*. The partial derivatives $\partial/\partial x$ and $\partial/\partial t$ have their usual meaning. The derivative dC/dL designates the total derivative in the usual sense, where it is considered that C is a function of L only and does not involve either x or t explicitly. Rossby (1945) uses d/dt to denote the rate of change with respect to an observer moving with group velocity.

$$\frac{\partial L}{\partial t} + \left(C - L\frac{dC}{dL} \right) \frac{\partial L}{\partial x} = 0. \tag{3}$$

Let the group velocity V be defined by the equation

$$V = C - L(dC/dL). \tag{4}$$

According to (3) and (4) *an observer traveling with group velocity records a constant wave length.* If dC/dL is positive, then $C > V$, and the observer is continually overtaken by individual waves.

This elegant derivation of the group velocity was first given by Lamb (1932, p. 382). Rossby (1945) derives equation (4) by equating the rate of increase of wave crests within a certain distance Δx to the excess of waves entering at x over those leaving at $x + \Delta x$.

For the case of low waves in deep water the classical equations

$$C \equiv \frac{L}{T} = \left(\frac{gL}{2\pi} \right)^{\frac{1}{2}} = \frac{gT}{2\pi} \tag{5}$$

apply, since the period is assumed to be a slowly varying function of time and distance. Equations (4) and (5) lead to the well known formulas

$$V = C/2 = gT/(4\pi). \tag{6}$$

Equations (3) and (5) give

$$\frac{\partial T}{\partial t} + V\frac{\partial T}{\partial x} = 0, \tag{7}$$

so that an observer traveling at group velocity records constant wave period. In a wave train in which individual waves (or crests) are neither created nor destroyed, the period as a function of time and distance must satisfy equation (7).

Equation (7) can be solved by the method of Lagrange. One solution,

$$T = \text{constant},$$

is of no further interest; the other solution,

$$T = f(t - x/V), \qquad \text{or} \qquad t - x/V = F(T), \tag{8a, b}$$

contains an arbitrary function, which depends upon the choice of coordinate axes.

According to equation (7) the period T, but not necessarily the group velocity V, remains constant relative to an observer traveling at group velocity. For surface waves in deep water, however, the group velocity depends on period only (equation 6), and, as long as T is constant, V must be constant.

Assume that a train of waves is generated by a sudden disturbance,[7] and let t and x designate the time and radial distance relative to this disturbance (fig. 3). Then the path of an observer traveling from the initial disturbance with constant group velocity V is given by

$$x = Vt \tag{9}$$

and the arbitrary function $F(T)$ in equation (8b) must vanish. The solid lines in fig. 3 represent the paths of two observers traveling at group velocities V_1 and V_2, respectively, and recording constant wave periods $T_1 = 4\pi V_1/g$ and $T_2 = 4\pi V_2/g$ (equation 6). The dashed lines represent the paths of individual waves. Fig. 3 shows that the individual wave increases continuously in period and velocity.[8]

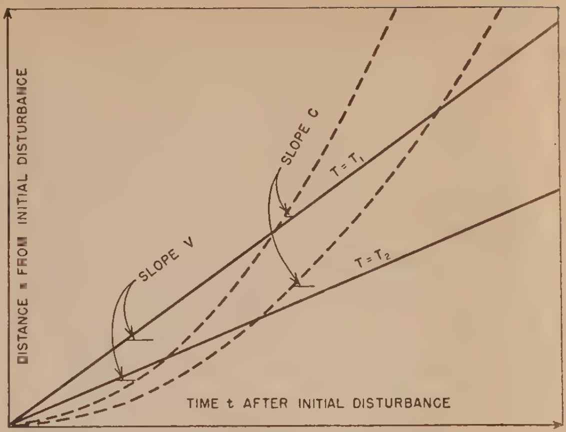
DISTANCE x FROM INITIAL DISTURBANCE
TIME t AFTER INITIAL DISTURBANCE
SLOPE C
SLOPE V
$T=T_1$
$T=T_2$

FIG. 3. Solid lines, paths of two observers each traveling with constant group velocity; dashed lines, paths of two individual waves. At the intersection of dashed and solid lines the slope of the dashed line equals twice the slope of the solid line, in accord with the equation $C = 2V$.

Combining (6) and (9) gives

$$T = \frac{4\pi}{g} \frac{x}{t}, \tag{10}$$

which has been derived independently by Rossby (1945). This solution is the same as that for the Cauchy-Poisson wave problem dealing with impulsive generation of waves (Lamb, 1932, pp. 384–398).

According to equation (10) the fast, long-period waves travel in front of the wave train and are followed by waves of gradually diminishing periods. The change of period with time at a fixed locality is found by partial differentiation:

$$\frac{\partial T}{\partial t} = -\frac{4\pi}{g}\frac{x}{t^2} = -\frac{T}{t}. \tag{11}$$

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[7] The exact nature of the initial disturbance need not be considered, as long as the initial surface deformation can be assumed to resolve quickly into a train of regular waves. Such an assumption appears justified by an exact analysis involving Fourier integrals (Lamb, 1932, pp. 384–394).

[8] A line integral between the origin and any point in the t,x-plane can be taken either along the curves denoting the travel of individual waves or along the straight lines denoting the path of an observer traveling with constant group velocity. The former alternative may appear to have greater physical reality; the latter alternative is preferable from a mathematical point of view. The straight lines are the 'rays' in the Hamilton-Jacobi wave theory.

Combining (10) and (11) leads to the interesting equations

$$x = \frac{gT^2}{4\pi(-\partial T/\partial t)}, \quad t = \frac{T}{(-\partial T/\partial t)}, \qquad (12a, b)$$

so that the distance x and time t can be determined if two quantities are known: the period T and the decrease of period with time, $-\partial T/\partial t$. Both quantities can be obtained from wave records. Equations (12) form the basis of the method for locating and tracking storms by means of the forerunners. They have been derived under the assumptions (a) that the effective distance and duration of generation are large compared with the total travel distance and travel time, (b) that individual waves are neither created nor destroyed, and (c) that the resulting wave pattern varies slowly with time and distance. The third assumption must be modified if the existing wave pattern is the result of two or more disturbances.

4. Conservative waves from multiple disturbances

Let t_s designate the time of a disturbance, t_w the time when waves of period T are recorded. Substituting

$$t = t_w - t_s \qquad (13)$$

into equation (10) gives

$$T = \frac{4\pi}{g}\frac{x}{t_w - t_s}, \qquad (14)$$

which is shown by the curve AA′ in fig. 4.

A second disturbance, at a time $t_s + \Delta t$ and distance $x - \Delta x$ from the wave station, generates a second train of waves. Periods of the second train are given by the equation

$$T' = \frac{4\pi}{g}\frac{x - \Delta x}{t_w - (t_s + \Delta t)} \qquad (15)$$

and are represented by the curve BB′ in fig. 4.

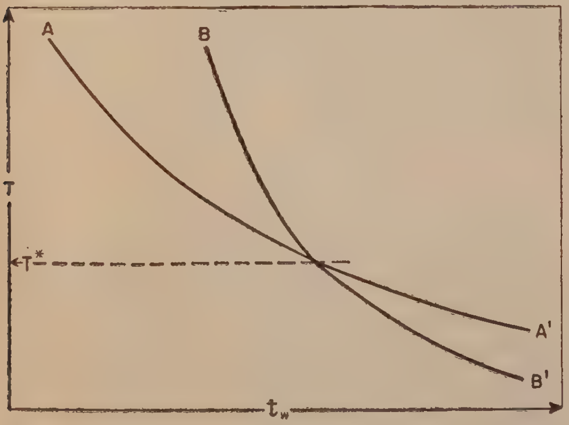

FIG. 4. Wave period T as a function of time t_w at a fixed station. At some instant the wave trains due to two distinct impulses have the same period, designated by T^*.

At any time t_w,

$$T' - T = \frac{4\pi}{g}\frac{\Delta t}{t - \Delta t}(V - \bar{U}) \qquad (16)$$

where

$$V = -x/t \qquad (17)$$

is the group velocity and

$$\bar{U} = -\Delta x/\Delta t. \qquad (18)$$

The minus sign appears in the last two equations because the x-axis is now drawn opposite to the direction of wave propagation. At the point where the curves AA′ and BB′ intersect one another

$$T = T' \equiv T^*, \quad \bar{U} \equiv V^* = gT^*/(4\pi), \quad (19a, b)$$

the last term following from equation (6); furthermore T' is longer than, equal to, or shorter than T according as V^* is larger than, equal to, or smaller than $\bar{U}$.

Equation (10) applies separately to each of the two wave trains simultaneously present at the wave station but does not apply to the resulting interference pattern, as the wave period and wave length of the interference pattern are no longer slowly varying functions of x and t. The definitions of L and T given in the previous section must be interpreted to apply to each of the wave trains, which can be separated from the interference pattern by a suitable method of harmonic analysis.

The reasoning can be extended to an infinite number of disturbances, separated by infinitesimal time intervals and distances, each sending out a wave train whose periods obey equation (10). As a result, neither one wave period nor two distinct wave periods are present at the wave station at any given time, but a *band* of wave periods.

5. Conservative wave theory applied to forerunners

It will be assumed that a storm system acts as a continuous, traveling source, applying an infinite number of impulses to the sea surface, each impulse giving rise to a train of waves in the sense described above. The speed $\bar{U}$ defined in equation (18) can then be identified with the rate of movement of the storm system toward the wave station.

The harmonic analyzer at the wave station draws a spectrogram of the resulting interference pattern The limits of the band and conspicuous feature within the band can be identified on consecutive records. If such a feature can be traced over a numbe of hours, say six hours, and if it is found to agree with equation (10), it may reasonably be attributed to definite conservative wave train, generated essentiall by a single impulse. The location of the impulse i then readily determined from equations (12).

To decompose the action of a storm upon the se surface into separate impulses may appear highly arbitrary, yet, in the author's opinion, a more rigorous analysis, perhaps following methods of statistical mechanics, would lead to similar results.

Care must be exercised in interpreting the significance of the limits of the period band. The shortest wave period is determined by the *earliest* storm action from which waves gathered sufficient energy to be perceptible at the wave station. The longest wave period is determined by the *latest* storm action from which waves are perceptible at the wave station. If a storm emits a broad spectrum of waves, as may indeed be the case, waves of period five minutes or longer, traveling as shallow-water waves similar to tsunamis (long ocean waves generated during submarine earthquakes and usually referred to as 'tidal waves'), constitute the theoretical upper limit of the period band (fig. 2).

The longest recorded waves do not reach this limiting period because the storm energy apportioned to the very long waves is small and because the response characteristics of the underwater unit are unfavorable. Equation (10) is therefore not applicable to the recorded upper limit as such, but in practice conspicuous features near the upper limit can be identified and used in computations. The lower limit, however, does not depend on the characteristics of the instrument, and equation (10) may be applied directly.

The use of forerunners for tracking storms is based on equations which were first derived in a study dealing with a different problem, namely, the increase in the period of waves traveling over large distances (Munk, 1947). It was shown that the same general theory can account for the observed increase in period of such widely different phenomena as swell, seismic surface waves, and tsunamis. Thus the fundamental notions appear to have a truly geophysical significance applicable to all waves traveling for long times and over long distances. The wide applicability derives from the general nature of equation (3), to which Rossby (1945) has applied the descriptive term 'wave equation of continuity.' Carl Eckart of the Institute of Geophysics, University of California, recently pointed out[9] that some of the results could also have been derived on the basis of the Hamilton-Jacobi wave theory. In the present paper, the only equations derived are those essential to the problem of storm tracking. A general development of the theory may be found in the paper on the period increase (Munk, 1947).

6. A graphical method for tracking storms

Equation (14) can be written in the form

$$\frac{4\pi}{g}\frac{1}{T} = \frac{1}{x}t_w - \frac{t_s}{x}. \tag{20}$$

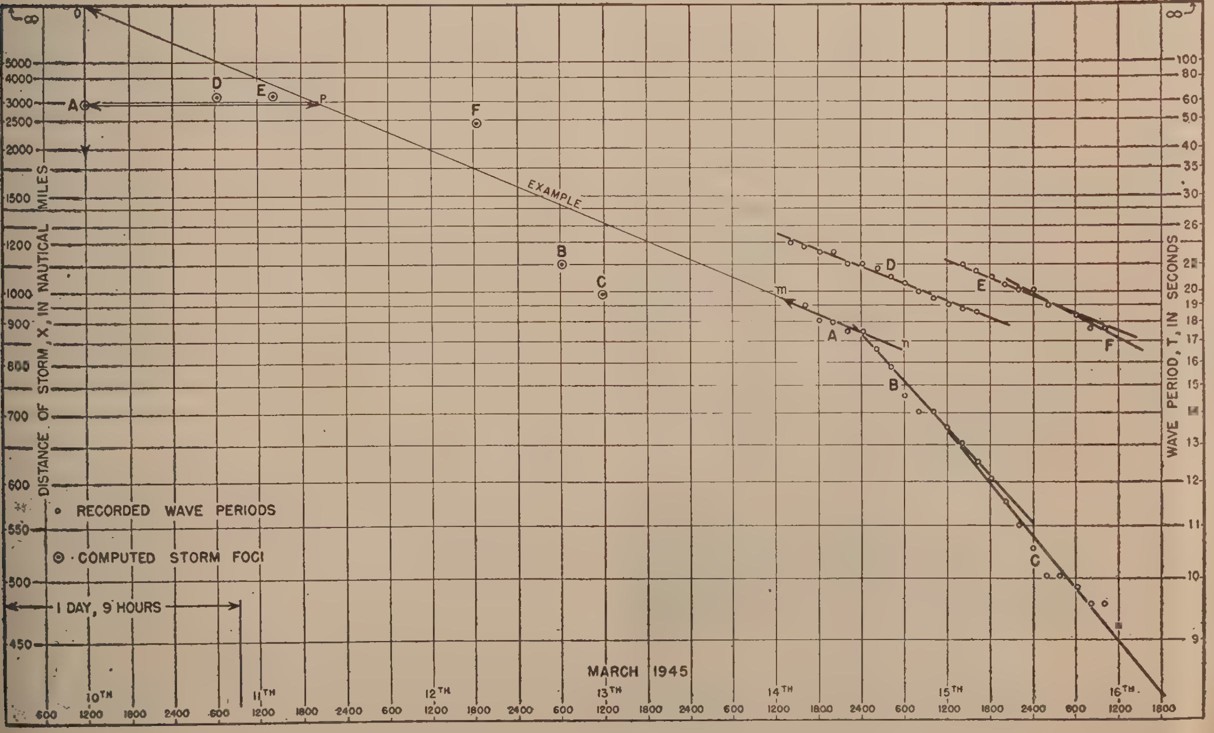

Fig. 5. Graph for computing storm foci (see section 6).

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[9] Verbal communication.

The problem is to evaluate x and t_s from a knowledge of T at various times t_w. If $1/T$, the inverse of the recorded period, is plotted against the recording time, t_w, then for any fixed wave train all points must fall along a straight line. The slope of the line equals $1/x$, and $t_w = t_s$ at the intercept of the line with $1/T = 0$. These relationships permit a simple graphical determination of x and t_s; the recorded wave periods and the computed storm positions are plotted on a single graph with the abscissa representing both t_s and t_w, the ordinate $1/T$ and $1/x$ (fig. 5). For convenience, the parameters $1/T$ and $1/x$ are designated by an inverted scale, so that T and x can be read off directly. The procedure is:

(a) Identify, in the recorded period spectrum, outstanding features such as the limits of the period band. The period T associated with each feature is plotted against t_w, the time when the wave was recorded. The open circles on the right side of fig. 5 were obtained in this manner for the upper and lower limits of the period band shown in fig. 6.

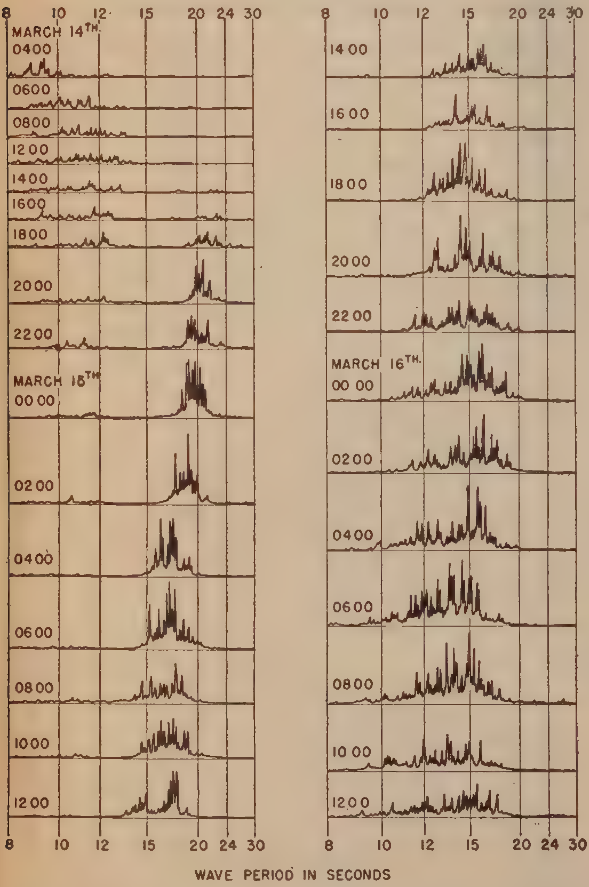

FIG. 6. Spectrograms of waves recorded during 14–16 March 1945 at Pendeen, England. Each spectrogram gives the distribution of energy for a 20-minute record. The records were taken at 2-hourly intervals. (From Deacon, 1946.)

(b) Connect any features which can be identified on at least three records and over at least six hours and which fall approximately along straight lines (lines A, B, $\cdots$ F in fig. 5).

To each of these lines on the x,t_w-diagram there corresponds a 'focal point' which gives the distance x of the storm at the time t_s. The foci are designated by the large circles on the left side of fig. 5, and each is marked according to the line with which it is associated. Thus the waves whose periods fall along line A were generated at the focus A. The six foci in fig. 5 indicate the movement of a storm system from a distance of almost 3000 miles at noon 10 March to a distance of about 1000 miles at noon 13 March. Fig. 5 illustrates the method whereby focus A is located:

(c) Extend line A until it intersects the line $T = \infty$, and draw a vertical. The vertical immediately gives t_s. The value of x is found by following a vertical downward until the horizontal distance AP between the vertical and the extended line through the observations corresponds to a time interval of 1 day, 9 hours. This time interval is the same for all foci and can be measured off in the lower left corner of the figure. Focus A is plotted, and the value of x is read from the scale on the left.

The time interval depends on the ratio of the two ordinate scales, which was arbitrarily chosen to be (50 nautical miles):(1sec). Point P, representing a period T and time t_w, has the same ordinate as point A, representing the distance x and time t_s; consequently x/T is equal to the ratio of scales. From equation (14),

$$t_w - t_s = \frac{4\pi}{g}\frac{x}{T} = \frac{4\pi}{g}\,\frac{50 \text{ nautical miles}}{1 \text{ sec}}$$
$$= 1.17 \times 10^5 \text{ sec} = 1 \text{ day, 9 hours.}$$

The entire derivation is completely determinate, and no arbitrary constants or functions have been introduced to fit the data. The examples in the next section will show that the calculations not only give the correct order of magnitude but also permit the location of storm positions to a considerable degree of accuracy.

The following additional rules follow from equations (19):

(d) The average speed of the storm system between the positions represented by foci A and B equals

$$\bar{U} = V^* = gT^*/(4\pi) \qquad (19b)$$

where T^* is the period at the intersection of the two straight lines A and B. Numerically $\bar{U} = 1.5\ T^*$ if $\bar{U}$ is given in knots and T^* in seconds. Any *abrupt* change in slope of the line representing a boundary of the period band is the result of an intersection of two such

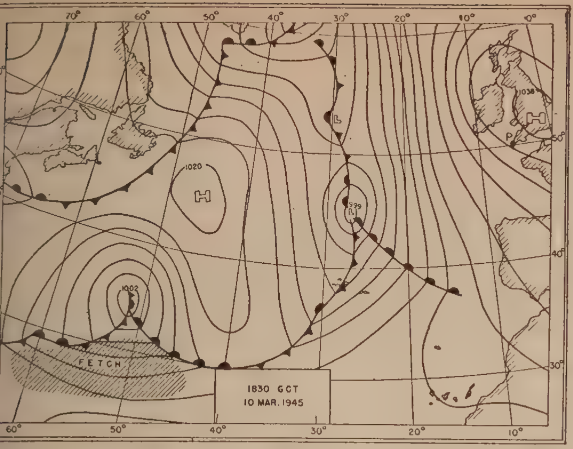

FIG. 7. Surface weather map for 10 March 1945. Fronts are resented in the conventional manner, and isobars are labeled millibars. Point P denotes the wave station at Pendeen, gland. Figs. 7–10 show the passage across the Atlantic Ocean the storm for which the wave spectrograms are shown in fig. 6.

es and can at once be interpreted in terms of the te of movement of the storm system.

(e) A *gradual* increase of slope can be formed only an envelope from a family of lines from adjoining ci. This situation arises only when the storm center decelerating, $\bar{U}$ decreasing according to equation 9b), where T^* is now the recorded period along the velope.

Examples based on records from Pendeen, England

14–16 March 1945.—Fig. 6 shows a set of period alyses obtained by methods discussed in section 2. e band of gradually diminishing periods is the result an intense storm which formed on 10 March 1945 the coast of Cuba, 3000 miles from Pendeen, and veled in a general northeast direction, passing st of the British Isles. Four representative weather ps are shown in figs. 7–10.[10] The positions indicated the 'fetches' were determined according to the rules veloped for wave forecasting.[11] It should be noted at the fetch lengthened during the time interval tween $18^{h}30^{m}$ 11 March and $18^{h}30^{m}$ 12 March.

The first indications of the storm on the wave record some 'low-frequency noises' at 14^{h} 14 March. that time visual observations at Pendeen revealed ly the presence of 10-sec and 12-sec waves from other source; the long forerunners of the swell were low to be visible. The upper and lower limits of the riod band of these forerunners have been read from e record and plotted in fig. 5. The positions of the six i A, B, ⋯ F have been determined by means of the aphical method described in the preceding section.

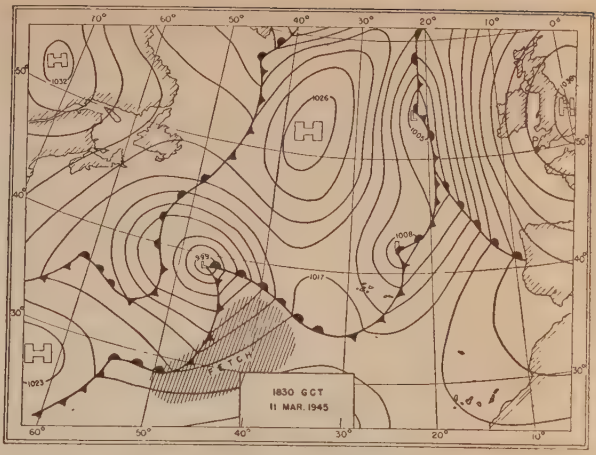

FIG. 8. Surface weather map for 11 March 1945.

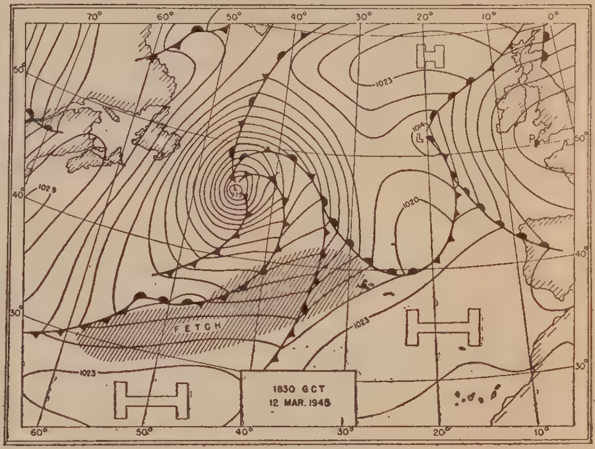

FIG. 9. Surface weather map for 12 March 1945.

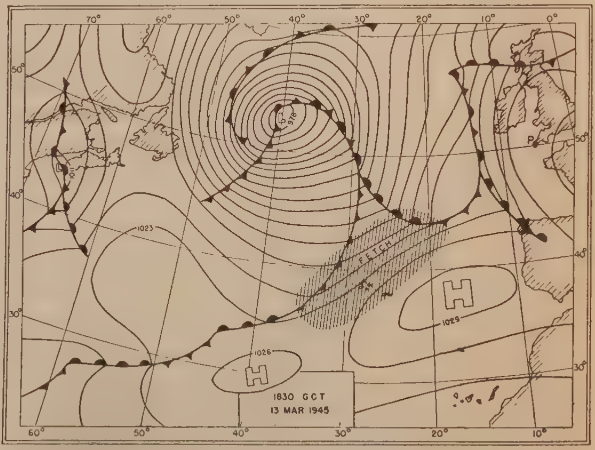

FIG. 10. Surface weather map for 13 March 1945.

The information taken from the weather maps and the periods recorded at the wave station have been replotted in fig. 11 to emphasize the similarity, with

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[0] The weather maps were drawn and analyzed at the U. S. vy Weather Central, Washington, D. C.

[1] Hydrographic Office, U. S. Navy, "Wind waves and swell; nciples in forecasting," H. O. Misc. No. 11,275, 61 pp., 1944.

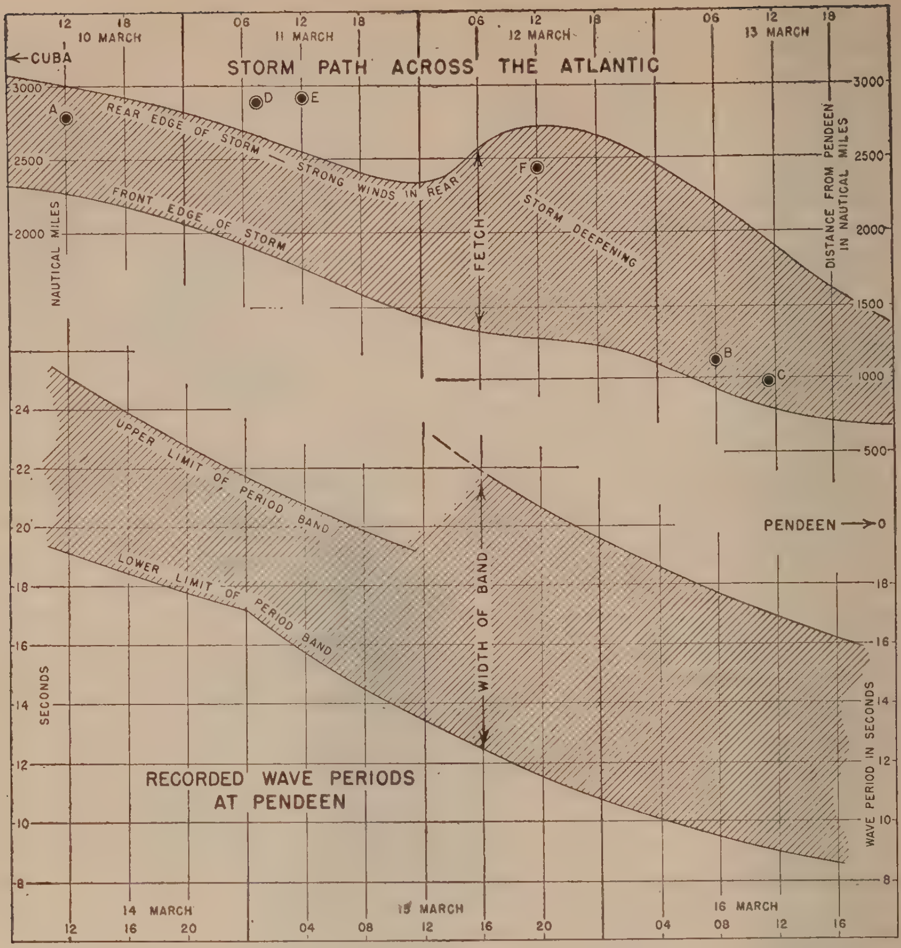

FIG. 11. Comparison of storm path with period band. The shaded band in the upper part shows the movement of the storm syste toward the wave station. The forward and rear edges of the storm were determined from 6-hourly weather maps, of which every four map is shown in figs. 7–10. The computed storm positions (foci) are marked A, B, ··· F. The limits of the period band in the low part were determined from the wave spectrograms shown in fig. 6.

regard to both shape and width, between the storm path and the period band. The computed positions, designated by A, B, ··· F, agree fairly well with the information on the weather maps, especially if it is remembered that the foci were obtained from theory without the introduction of any arbitrary constants. The foci A, B, and C were computed from the lower limit of the period band and seem to correspond to the forward edge of the fetch; D, E, and F were computed from conspicuous features near the upper limit of the period band and give the approximate position of the rear edge of the fetch. It can be seen, however, that focus A in the upper part of fig. 11 is located 500 miles behind the storm front and the other two foci about 200 miles behind the front. These discrepancies must be expected, since waves generated at the front itself could not gather sufficient energy to be perceptible at the wave station; furthermore, the distance between the point of wave origin and the storm front must be larger for the furthest disturbance, which almost 3000 miles from Pendeen.

27–29 April 1945, fig. 12.—The waves are the resu of a cyclone which centered over Newfoundland ear on 23 April, when an 800-mile fetch in the warm sect extended from Bermuda toward east-northeast. I noon on 24 April the storm had moved to mid-Atlanti where it was reinforced by a secondary cold fror The strong winds were blowing toward Africa, so th the fetch toward Pendeen was considerably weakene This condition persisted for about a day until noon 25 April, when a secondary trough merged with t main trough, and an intensification of the stor occurred, strong winds blowing toward the wa station (see map in fig. 12). This intensification, whi followed an interval of relatively weak generation waves, is reflected in the spectrograms as a new featu marked F in fig. 12. This feature is quite distinct fro the main period band. It will be noted from the low

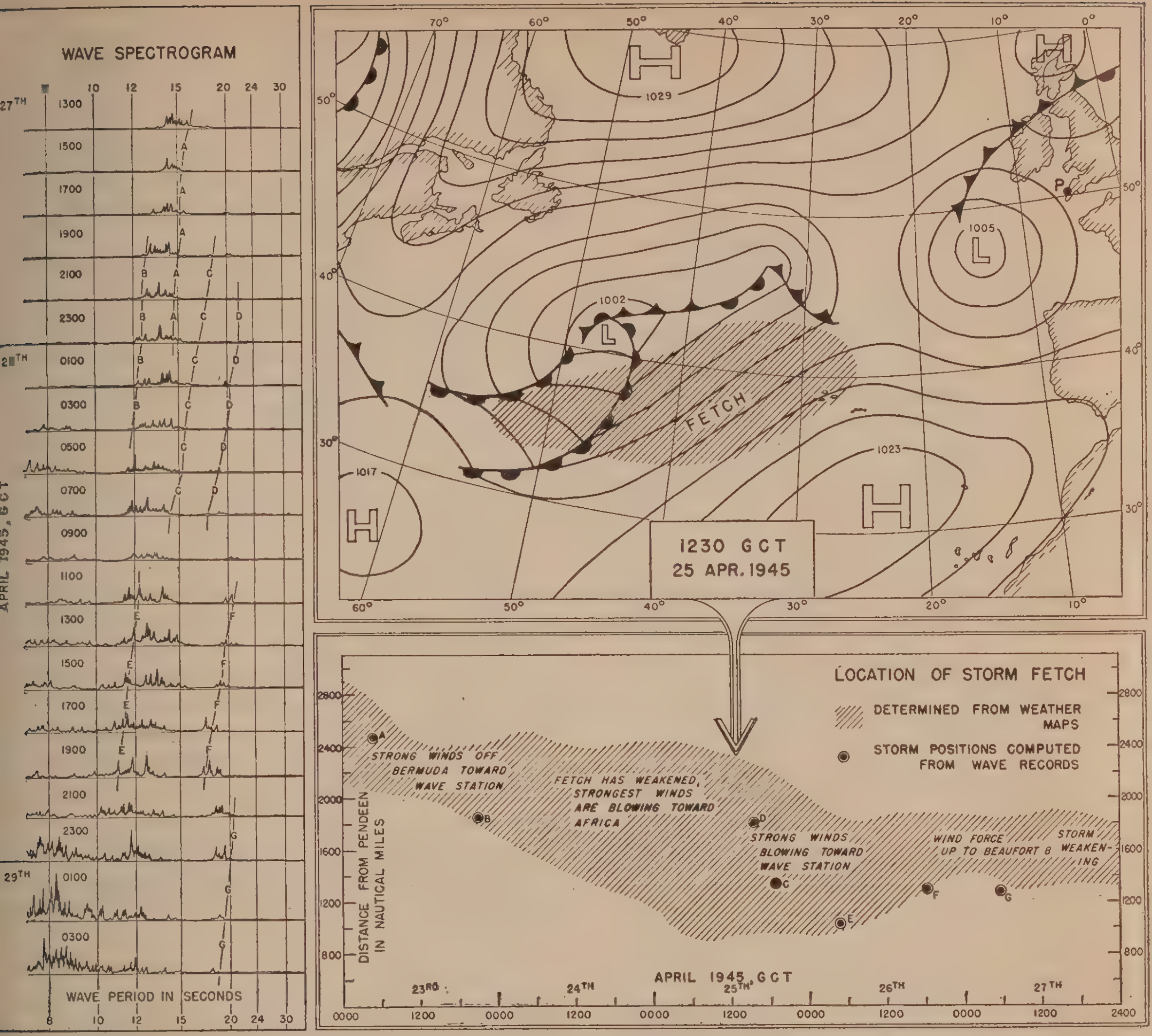

Fig. 12. Application of storm-tracking method to wave records of 27–29 April 1945. The period spectrograms recorded at Pendeen are own on the left. Significant features on adjoining records are connected by dashed lines, marked A, B, · · · G. The corresponding foci shown by the circles in the diagram at the lower right, where the shaded band gives the path of the storm determined from weather ps. One of these weather maps is shown at the upper right.

ht part of fig. 12 that the focus F falls in the fetch at e time of intensification.

The storm then remained stationary and intensified rther, the wind attaining a force up to Beaufort 8 rly on 27 April. On the spectrograms the feature arked G can be associated with the region of ghest wind. On 27 April the cyclone started to ove northward, weakening and undergoing fron-
lysis.

According to fig. 12 the computed foci are in good reement with information contained on the weather aps. All seven foci fall into intervals of strong winds, d no features which would fall into time intervals weak winds could be identified on the wave records.

18–21 February 1945, fig. 13.—This example illusates the application of the method to a more complex meteorological situation. Two storm systems, which existed simultaneously, could be identified and traced separately.

On 15 February the development of a cyclone started off the east coast of the United States. On 17 February the center of the cyclone had reached mid-Atlantic, and an unusually well defined 1000-mile fetch in the warm sector was pointing directly toward the wave station. At the same time a new low-pressure area had just moved off the east coast of the United States and formed a second fetch immediately north of Bermuda (fig. 13). As the first storm stagnated and veered northward toward Iceland, Pendeen came under the influence of the fetch in the cold sector, which remained at about the same distance from Pendeen. In the meantime the fetch in the warm sector

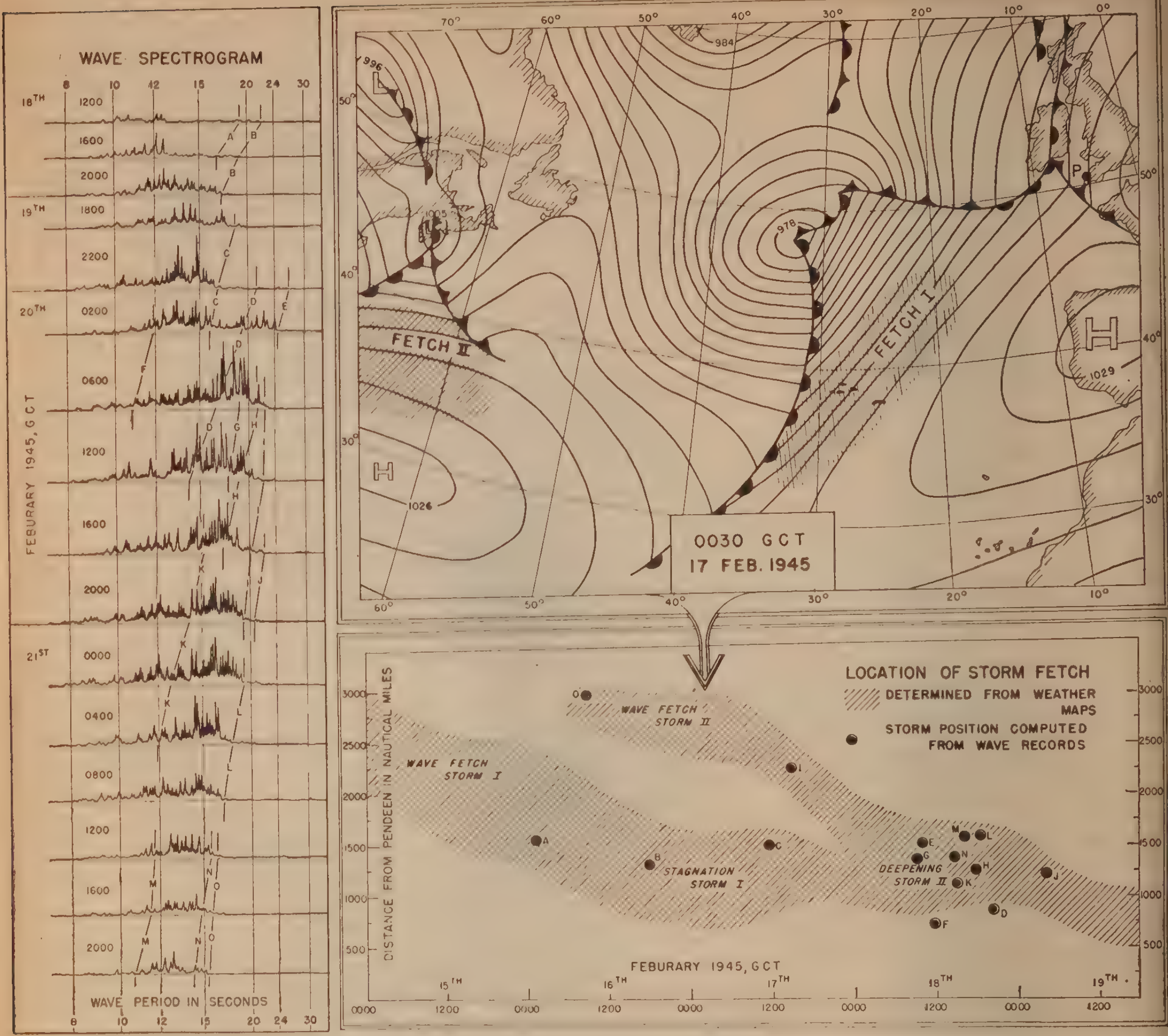

Fig. 13. Application of storm-tracking method to wave records of 18–21 February 1945. The presentation of the data is the same as that used in fig. 12, except that only alternate spectrograms are shown in the left part of the figure.

of the second storm moved slowly eastward, and on 18 February this and the fetch remaining from the first storm appeared as a single generation area. By 19 February the first storm had undergone complete frontolysis. The only remaining fetch was that in the cold sector of the second storm, which was moving northward toward Iceland.

The spectrograms shown in fig. 13 are more complicated than those in the preceding examples, and the interpretation is much more difficult. The first three foci fall in the first storm as it moved across the Atlantic. Foci D to H are associated with wave trains that were formed as the first storm veered northward and its fetch was joined with the fetch of the second storm. Only by that time had the main period band moved sufficiently into the lower periods to permit identification of a wave train, F, from the dista second storm. Foci J to N originated from the joi fetch existing from 18 to 19 February, but focus had its origin in the second storm system, when it w still 3000 miles from the wave station.

8. Conclusions

Altogether eleven meteorological sequences ha been studied by means of the Pendeen wave record Of these the three best cases have been selected f examples in this report, but in all instances the agre ment between computations based on the wave recor and the information on the weather maps was e couraging. In one instance, 26 June 1945, waves fro a hurricane off the coast of Florida were faintl recognizable above the disturbance caused by oderate local storm. Attempts have also been made analyze wave spectrograms from Woods Hole, assachusetts, but there the time interval between cords equaled six hours. To identify the same atures on subsequent records was consequently al- ost impossible. For this reason it is not known at this ne whether the methods of this report can be applied wave records taken at stations located to the rear of e storms.

It is hoped that theoretical studies dealing with the opagation of *energy* by the forerunners (Sverdrup, 47) will lead to an interpretation of the spectrogram *linate*, which has received no attention so far but ust be related to the storm intensity. Considerable ogress can also be expected from the use of a deeper derwater unit. It may be possible to record fore- nners with periods up to 60 sec and corresponding oup velocity of 2200 nautical miles per day. Informa- n transmitted by these very early forerunners uld not only reach the wave station sooner but, ording to experience gained so far, would also be re accurate.

The relatively long interval between the time the ves are generated and the time they are recorded the wave station is a disadvantage in the applica- n of the method. Therefore the practical use will be gely to verify or modify the interpretations already de on the basis of meteorological information. This uld be particularly useful for regions where the work of observing stations is widely spaced. In case of compact meteorological disturbances, such young hurricanes, the waves may well provide the t clue as to the existence of the storms. The ap- ation of the method is further enhanced by the sibility of determining not only the location of the rm but also its size, intensity, acceleration, and ne of its other characteristics. In this connection it uld be remembered that the wave pattern provides omplete picture, though a distorted one, of the ire wind distribution over the ocean, and our erpretation of this picture should improve with the ance of instruments, of theoretical studies, and of empirical experience. Not until many more situations have been analyzed will an evaluation of the usefulness of the method be possible. The results so far obtained demonstrate the feasibility of locating and tracking storms at distances exceeding 3000 miles and of making rough estimates regarding the size and character of these storms.

Acknowledgments.—Dr. H. U. Sverdrup and Mr. Robert S. Arthur have contributed greatly to all phases of this investigation. I have also benefitted by opportunity to discuss the problem with Dr. C.-G. Rossby. I am greatly indebted to Mr. T. Saur for his assistance in the meteorological aspects of the problem and in the working-up of the data. The wave records have been kindly placed at our disposal by the Oceanographic Research Group, Admiralty Research Laboratory, Teddington, England. The cooperation of Captain H. T. Orville, USN, in providing us with the necessary meteorological data and his encouragement in the investigation are gratefully acknowledged.

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REFRACTION OF OCEAN WAVES: A PROCESS LINKING UNDERWATER TOPOGRAPHY TO BEACH EROSION

WALTER H. MUNK AND MELVIN A. TRAYLOR
Scripps Institution of Oceanography[1]

ABSTRACT

Waves out at sea, though usually forming a complex pattern, have essentially the same characteristics over large distances. Upon entering shallow water, these waves are transformed under the influence of bottom features, and such transformations may be so marked that breaker heights may vary greatly over short distances along the shore. The effect of bottom features upon waves can largely be interpreted in terms of a simple physical process—wave refraction. In turn, wave refraction may be responsible for alteration of the bottom features by accumulation or removal of sediments and, in this manner, be an important factor in beach erosion.

In this report the role of wave refraction is first reviewed in the light of other processes affecting the transformation of waves in shallow water. The mechanism of refraction is illustrated by means of a few idealized examples, such as the refraction pattern along a straight uniformly sloping beach, over a submarine canyon and ridge, and around a headland. Next it is shown that extreme variations in breaker height along the beach north of La Jolla, California, can be computed for typical swell conditions, taking the complex local bottom topography and the orientation of the coastline into consideration. These changes are computed from refraction diagrams for typical swell conditions, and they compare favorably with observed changes in wave height, thus indicating that wave refraction is the primary mechanism controlling changes in wave height along a beach, and that friction, diffraction, and other processes can be of secondary importance only. Finally, it is noted that the transportation of sediments is dependent upon longshore currents, rip currents, and horizontal diffusion and that all these factors are greatly influenced by the existing refraction pattern.

INTRODUCTION

Waves may have traveled many days and for thousands of miles before they approach shore and become transformed under the influence of the ocean bottom. By that time the long, low, regular undulations, called "swell," may be all but hidden beneath a local chop. As soon as the swell enters shallow water, it "feels" bottom, and a striking rejuvenation takes place. This change occurs in water of depth less than one-half the wave length, where wave length is defined as the horizontal distance between adjacent crests. The wave velocity and length decrease while the height usually increases, so that the wave gradually steepens. As the waves approach the surf zone, this process of steepening accelerates suddenly—the crests rise sharply from the water surface, become peaked, and break.

The changes just described are most noticeable for a swell from a distant storm. Waves formed by a near-by storm, or by winds blowing directly toward the coast, have already considerable steepness out at sea; the transformation in shallow water, though similar, is therefore much less pronounced.

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 307. This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the Navy Department under contract with the University of California.

Only the period, defined as the time interval between the appearance of two successive crests at a fixed point, remains constant as waves travel into shallow water. According to theory, well substantiated by observation, wave velocity and length depend almost entirely upon wave period and depth (see the Appendix). For a regular wave system the velocity and length will therefore be constant along any given depth contour.

The discussion so far has dealt with changes in the character of the waves which are the direct result of changes in velocity and length. Except under very special conditions, the wave height will, however, not be uniform along any given depth contour, because the effect of refraction over an irregular bottom enters. This effect causes waves to bend, and the bending of the wave crests in turn affects the wave height. With irregular bottom topography, waves are bent differently at different sections of a beach, and the wave height will vary along the beach. The present study is concerned principally with a discussion of the refraction effects.

The refraction of ocean waves and other problems dealing with the transformation of waves in shallow water have been studied intensively during the war in connection with the development of a method for forecasting surf conditions for amphibious operations.[2] Practically all changes in the character of the waves in shallow water can be accounted for theoretically by assuming conservation of energy and irrotational wave motion, and it has been shown that the conclusions based on theory are in goo agreement with observations.[3]

WAVE REFRACTION

THE PHYSICAL NATURE OF WAVE REFRACTION

Wave crests approaching a coastlin at an angle tend to swing parallel t shore (Fig. 1). This happens because th wave velocity decreases as the depth d creases, so that the portion of the cre nearer the shore moves slowly while th portion of the crest in deeper water race ahead. To illustrate this, consider tw surfboarders on the same crest, travelin along the lines *A* and *B* (Fig. 1). Sur boarder *B* always travels faster than and the two tend to become more nearl aligned with the shoreline as they trav into shallow water.

The process is similar to the one cau ing the bending of light rays in optic systems and has therefore been terme "refraction." In the case of straigh parallel contours, the analogy can b carried further, because the changes i direction of light waves and ocean wave are governed by Snell's law:[4]

$$\frac{\sin \alpha}{\sin \alpha_0}=\frac{C}{C_0}, \qquad \text{(1}$$

where α is the angle between the wav crest and the contours at any depth, the wave velocity at the same depth, an the parameters with subscript o refe only to deep water where the directio and velocity are constant.

REFRACTION DIAGRAMS

In the case of a more complicated bo tom topography for which the dept contours are not straight and paralle changes in wave direction and height can be found graphically by constructing a "refraction diagram," a term first used by O'Brien and Mason.[5]

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[2] "Breakers and Surf, Principles in Forecasting," *Hydrographic Office, U.S. Navy, No. 234* (November, 1944).

[3] H. U. Sverdrup and W. H. Munk, "Theoretic and Empirical Relations in Forecasting Breake and Surf," *Trans. Amer. Geoph. Union,* Vol. XXVI No. 6 (December, 1946), pp. 828–36.

[4] Pp. 6–7 of ftn. 2.

A refraction diagram is one on which the position of wave crests at the sea surface is shown by a series of lines. These are evenly spaced in deep water—that is, in water of depth greater than half the wave length. Beyond this depth the effect of bottom contours on any of the wave characteristics is negligible. At shallower depths the relation between wave velocity and water depth is known (see Appendix), and a refraction diagram can be constructed by advancing various points on a crest through distances determined from any chosen time interval and the average depth. The direction of advance is drawn normal to the crest. In Figure 1, for example, the chosen time interval is one wave period, and the distance A_0—A'. The distance B_0—B' represents the advance of point B during the same time interval, but for the average depth between B_0 and B'. The lines A_0—A' and B_0—B' are normal to the wave crests. By locating a set of points, A', B', C', ... , the new crest can be found with sufficient accuracy by drawing a smooth line through these points. Advancing one wave length at a time, the crests may be carried into any depth of water desired, and the completed diagram shows the continuous change in the direction of a wave advancing from deep into shallow water.

Description of a practical procedure for constructing refraction diagrams, together with the necessary graphs and tables, can be found in the forecasting manual.[6] The completed diagram can be interpreted in one of two ways: (1) As a series of lines representing the positions of a *single* wave crest at various times as the crest advances toward shore. Crest interval is then defined as the interval between these times. In Figure 1 the crest interval equals one wave period. (2) As a series of lines representing the position of certain wave crests at a *single instant;* a crest interval of *one* wave length means that every crest is represented (Fig. 1), because the advance of any point on a crest during one wave period equals one wave length by definition. A crest interval of *two* wave lengths means that only every second wave crest is shown; a crest interval of *one-half* wave length, that the position of every crest and trough is shown.

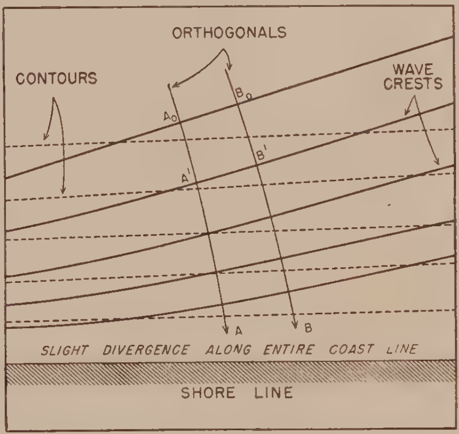

FIG. 1.—Refraction of waves along beach with straight parallel depth contours. The wave crest along the orthogonal *B* is always in deeper water than along *A* and therefore moves with greater velocity. As a result, the waves tend to turn parallel to shore.

EFFECT OF REFRACTION ON WAVE HEIGHT

Wave height is defined as the vertical distance between crest and trough. In order to evaluate the effect of refraction on wave height, a set of orthogonals, that is, a family of lines which are everywhere perpendicular to the wave crests, must be constructed. The lines A_0–A and B_0–B in Figure 1 are orthogonals; they may be visualized as the wakes behind two surfboards which are continuously oriented normal to the crest, that is, in the direction of wave motion. Assuming that the wave *energy* is transmitted in the direction of wave motion, the total flow of energy between two orthogonals must remain constant. Thus if orthogonals *converge*, the crests are *compressed*, and the energy per unit crest length is relatively *large;* if orthogonals *diverge*, the crests are *stretched*, and the energy per unit crest length is relatively *small*.

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[5] "A Summary of the Theory of Oscillatory Waves," *Technical Report No. 2, Beach Erosion Board* (1940).

[6] Pp. 31–34 of ftn. 2.

For practical purposes one must deal with wave heights rather than with wave energies, but these are related. In deep water the height of oscillatory waves varies as the *square root* of energy, and this relation holds with good approximation in shallow water until the waves "peak" just prior to breaking. The breaking waves, with their sharp crests isolated by long flat troughs, have the appearance of so-called "solitary" waves, for which the height is proportional to the *cube root* of the energy. Let H designate the wave height and s the distance between adjacent orthogonals on the refraction diagram. Parameters with subscript 0 again apply in deep water, those with subscripts b at the breaker point, and parameters without subscript at any depth intermediary between deep water and the breaking-point. Then

$$\frac{H}{H_0} = \gamma K\,, \quad \frac{H_b}{H_0} = \gamma_b K_b\,, \quad (2a,\, b)$$

where γ and γ_b have constant values along a fixed depth contour, and where

$$K = \sqrt[2]{s_0/s}\,, \quad K_b = \sqrt[3]{s_0/s_b}\,, \quad (3a,\, b)$$

may vary along a depth contour and will be referred to as the "refraction factors." The complete derivation of these equations is given in the Appendix.

Any *variation* in wave height along fixed depth contour depends only upon the refraction factor. The variation can be computed from the change in distance between orthogonals according to equations (3), depending upon whether one deals with conditions in shallow water or along the breaker line. Again it should be stressed that the absolute wave height depends also upon several other factors which are implicitly contained in the parameters γ and γ_b of equations (2) (see Appendix).

Equations (2) are derived from the postulates that the energy flows along orthogonals and that energy is conserved. This in turn implies two assumptions: (1) the effect of *diffraction* (which would bring about flow of energy across orthogonals from region of high waves to regions of low waves) can be neglected and (2) the effect of bottom friction is negligible. The validity of these assumptions is borne out by the good agreement between computed changes in breaker height according to equations (2), and observations along the beach north of La Jolla, California (Fig. 16). There has been a tendency in the literature to emphasize the effect of bottom friction on wave motion and other wave characteristics. Not only the evidence presented in this paper, but also studies dealing with the generation of waves by wind,[7] and with absolute changes of wave height in shallow water and the dynamics of breaking waves,[8] indicate that wave motion in general is not appreciably affected by frictional processes.

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[7] H. U. Sverdrup and W. H. Munk, "Empirica and Theoretical Relations between Wind, Sea and Swell," *Trans. Amer. Geoph. Union*, Vol. XXVII No. 6 (December, 1946), pp. 823–27.

[8] Pp. 830–32 of ftn. 3.

REFRACTION TYPE EXAMPLES

Beach with straight and parallel depth contours.—For this simple case the change in wave direction can be expressed analytically by equation (1). Figure 1 is a schematic drawing of wave refraction along a straight coastline with parallel depth contours. Plate I, *A*, is an aerial photograph showing long waves from the south-southwest coming into the beach north of Oceanside, California. There is a divergence of the orthogonals indicated by the values of *s* computed from the equation[9]

$$\frac{s}{s_0}=\frac{\cos\alpha}{\cos\alpha_0}. \tag{4}$$

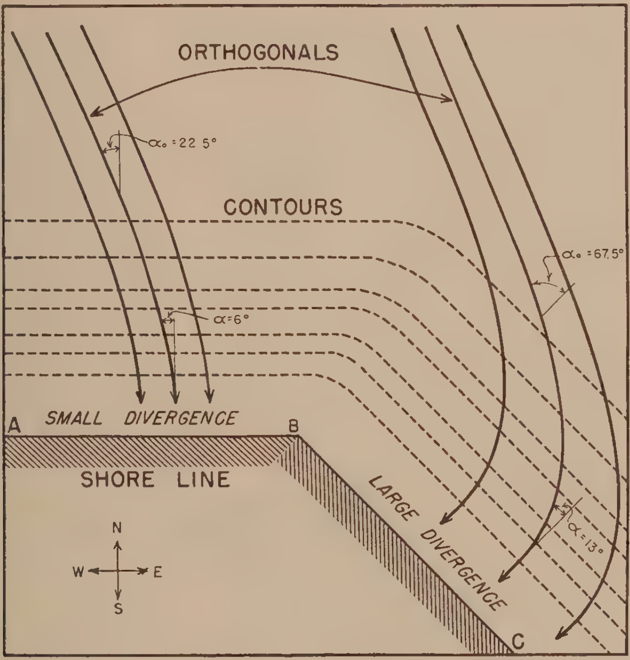

FIG. 2.—Refraction of waves along two sections of straight beaches with different exposures. The divergence along section *A–B* is less than along *B–C*, and the wave height along *A–B* exceeds therefore the wave height along *B–C*.

Combining equations (1), (3), and (4) leads to

$$\left.\begin{aligned} K &= \left[\frac{\cos^2\alpha_0}{1-\left(\frac{C}{C_0}\sin\alpha_0\right)^2}\right]^{1/4}, \\ K_b &= \left[\frac{\cos^2\alpha_0}{1-\left(\frac{C_b}{C_0}\sin\alpha_0\right)^2}\right]^{1/6}, \end{aligned}\right\} \tag{5a, b}$$

where C/C_0 is found from equation (A7) in the Appendix.

Waves coming from an angle into a beach with straight and parallel depth contours are reduced in height according to equations (5), but the reduction is uniform along the entire beach, and no *variation* in wave height *along* the beach will result. As an example of variation in wave height, consider a coastline which forms a sharp bend at point B (Fig. 2). On both sides of point B the coastline and the depth contours are straight and parallel. Assume that waves of 14-second period come from the north-northwest. The angle α is drawn between the orthogonals and the bottom gradient, which is consistent with our earlier definition. Table 1 gives the computed direction and relative height at the 10-foot contour, which is assumed to lie outside the breaker zone. Along the beach section A–B, which is relatively exposed to the incoming swell, waves are about 50 per cent higher than along section B–C. This can also be seen from the fact that the divergence of orthogonals along A–B is less than the divergence along B–C (Fig. 2).

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[9] Pp. 20–21 of ftn. 2.

TABLE 1

Section of Coast Line (Fig. 2)	A–B	B–C
Wave angle in deep water (α_0)	22.5°	67.5°
Wave angle at 10-foot depth (eq. [1])*	6.0°	13.0°
Refraction factor (eq. [5a])	0.97	0.63

* The value of C/C_0 is obtained from "Breakers and Surf," *op. cit.*, Pl. I, and equals 0.25.

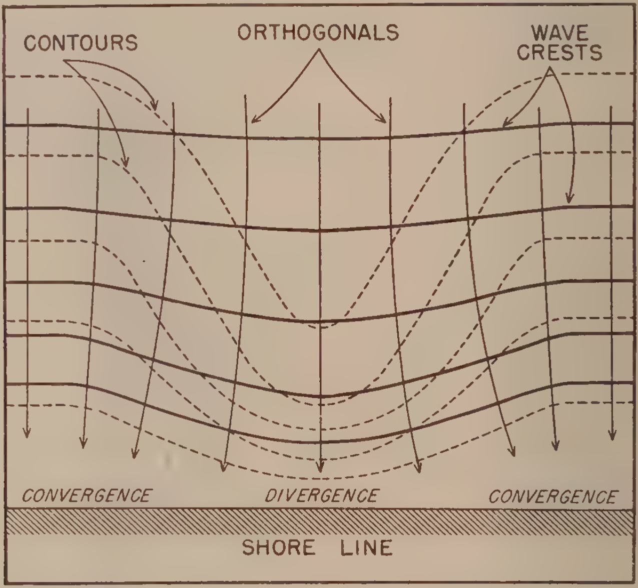

FIG. 3.—Refraction of waves by a submarine canyon. Waves move faster over the canyon than on either side of the canyon, resulting in divergence (low waves) over the mouth of the canyon and convergence (high waves) on either side.

Submarine canyons.—Portions of wave crests over the center of a canyon are in deeper water and move ahead faster than the portions on either side (Fig. 3). Consequently, the waves fan out, resulting in divergence (low waves) over the head of the canyon and convergence (high waves) on either side. Fishermen take advantage of this feature when they anchor near the head of a submarine canyon. Plate II is an aerial photograph of waves over the submarine canyon at Redondo, California. The approximate position of the canyon is indicated. The wave crests bend sharply over the canyon walls. Variations in wave height can be recognized by the prominence of the wave crests on either side of the canyon compared to the crests directly over the canyon and by the variation in the width of the surf zone.

Submarine ridges.—Underwater ridges near shore have an effect opposite to that of canyons. Waves passing over the ridge are in shallower water and are therefore retarded, and on either side waves move ahead, creating a convergence over the ridge (Fig. 4). This is borne out by frequent observations of unusually violent breakers over the shoal portion of underwater ridges. An aerial photograph take over the northern shore of Oahu, T.H. (Pl. I, *B*), illustrates the lagging of the wave crests over a submarine ridge and the resulting convergence. Figure 5 illustrates the same features over a sand bank opposite the mouth of Mission Bay, San Diego, California. In the case of Mission Bay the refraction pattern is somewhat affected by the tidal flow through the outlet.

Abrupt changes in depth along coral islands lead to particularly well-defined refraction patterns. Plate III shows two channels in the coral reef around Guam; the waves are seen to bend sharply ahead over the channels, where they are lower than on either side of the channels. The photograph also shows the formation of multiple crests just inside the reef, a phenomenon often observed in regions of abrupt depth changes, and one which has never been properly explained.

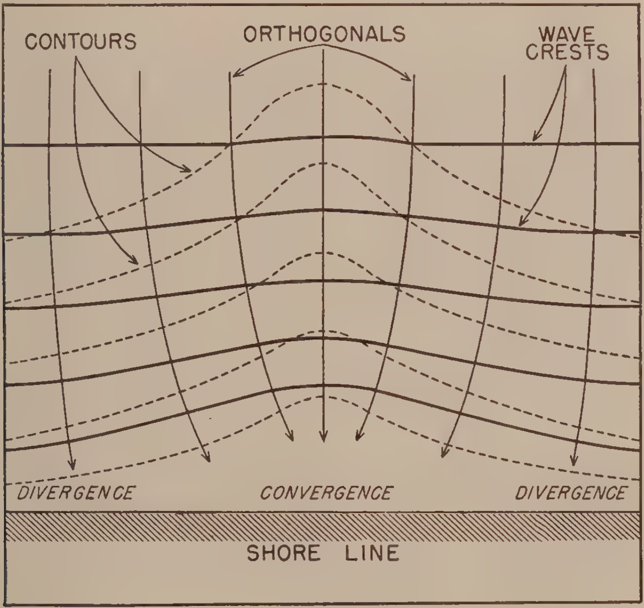

FIG. 4.—Refraction of waves by a submarine ridge. Directly over the ridge waves lag behind, and on either side waves move ahead, creating a convergence (high waves) over the ridge.

Headlands.—Since waves are retarded by shallow water, they will bend around headlands, points, and jetties. Plate IV, *A*, shows an irregular train of waves turning around Point Loma into San Diego Bay.

Under special conditions, such as portrayed in the aerial photograph of the hook of Cape Cod, Massachusetts (Pl. IV, *B*), waves may bend 180°, or even more, before they break. Such extreme refraction is associated with a very large divergence, which explains the shelter usually provided by protruding land masses.

Bays and islands.—Waves will be retarded along the sides of a bay but move relatively rapidly elsewhere. As a result, the crests will bend *into* the bay (Pl. V). The divergence will be largest at the sides of the bay, least opposite the mouth, especially if waves head directly into the bay. In the case of small islands in the path of an advancing swell the resulting refraction pattern is more complicated (Fig. 6). Offshore in the lee of the island, wave trains which have bent around both sides of the island meet and pass through each other, and a confused cross-sea results.[10] Where the bottom shoals gradually near shore, then drops off steeply, waves may be bent so effectively around an island that the lee shore offers no protection whatsoever.[11] Some coral islands have these characteristics.

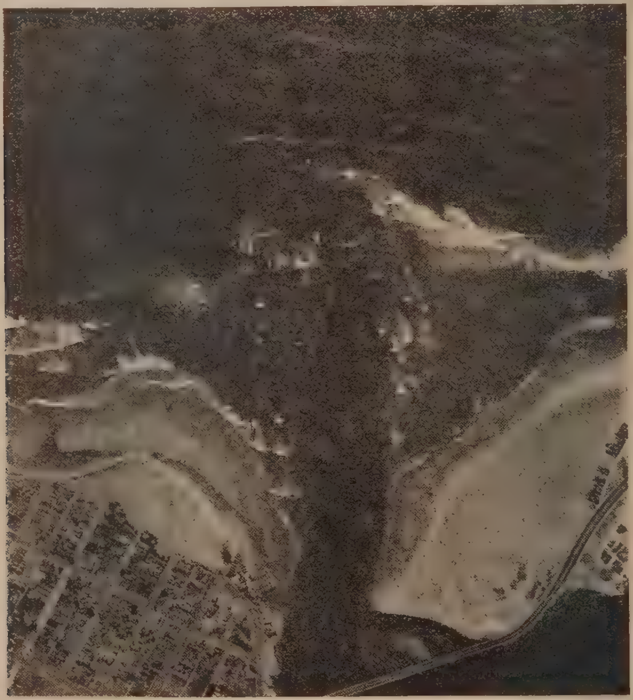

FIG. 5.—Refraction of waves over sand bar outside of Mission Bay, San Diego, California (cf. Fig. 4). The outflowing tide may have further strengthened certain features in the existing refraction pattern. (Official photograph, United States Navy.)

WAVE REFRACTION ALONG THE BEACH NORTH OF LA JOLLA, CALIFORNIA

ORIGIN OF WAVES REACHING LA JOLLA

In order to apply the principles of refraction to an actual situation, it is first necessary to determine the periods and directions of waves that will be encountered. For that purpose the character of the waves at La Jolla resulting from typical meteorological situations will be tabulated below. The paths and nature of the generating areas are shown schematically in Figure 7; the corresponding character of the waves at La Jolla, in Figure 7, *B*.

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[10] Pp. 12–18 of ftn. 2.

[11] Robert S. Arthur, "Refraction of Water Waves by Islands and Shoals with Circular Bottom-Contours," *Trans. Amer. Geoph. Union*, Vol. XXVII (April, 1946), pp. 168–77.

Situation A (*winter*).—Waves generated by cyclones originating at the east coast of Asia and moving along the usual cyclone path into the Gulf of Alaska:

Waves generated in the southern segments of these cyclones reach La Jolla in 2–5 days as a long-period (11–15 seconds) swell, with heights varying between 3–7 feet, according to the intensity of the cyclone. The wave energy reaching La Jolla is reduced by the offlying islands, especially San Clemente and Santa Catalina (Fig. 7, *A*). The cyclones often stagnate in the Gulf of Alaska, and the coasts of British Columbia, Washington, Oregon, and northern California will be hit by a heavy swell, whereas southern California will be protected by Point Conception, which cuts off La Jolla from waves from directions much north of WNW.

Situation B (*winter*).—Waves generated behind cold fronts that come into the coastal regions:

These waves have short periods (7–10 seconds), large heights (4–12 feet), and usually come from a W to NW direction.

Situation C (*summer*).—Waves generated by winds in the northeast periphery of the Pacific High:

Usually the period of the waves will vary from 6 to 9 seconds, the height from 2 to 5 feet. The common direction is from WNW to NW.

Situation D (*summer*).—Waves generated in the Southern Hemisphere:

The so-called "southern swell" comes from S to SSW, is of very long period (13–20 seconds), and is usually 3–5 feet high. This is the only direction from which waves can reach La Jolla without being broken up by offlying islands.[12] There is strong evidence that this swell has been generated by the winter storms of the Southern Hemisphere, but, owing to an almost complete lack of weather observations, this has not been verified.

Situation E (*spring*).—Wind waves generated in local low-pressure regions:

Local low-pressure regions, which are usually not forecast, give rise to W or NW winds with

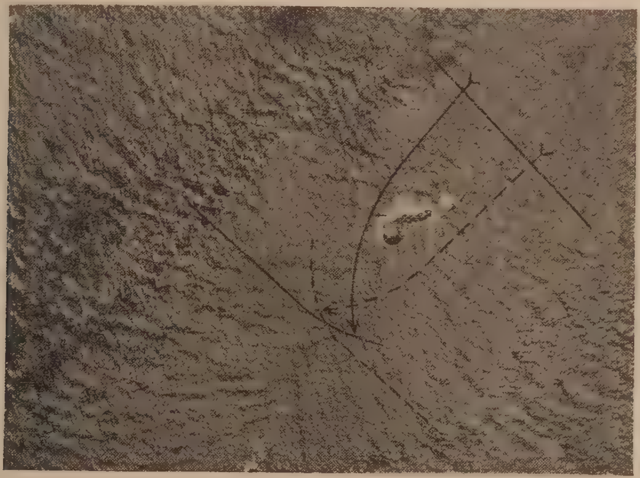

FIG. 6.—Refraction of waves behind a small island. The portion of the wave passing just to the right of the island is refracted to the left; the portion passing just to the left of the island is refracted to the right. The resulting crisscross pattern gives rise to a confused sea in the lee of the island, and the island may offer little or no shelter.

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[12] Plate I, *A*, is an aerial photograph of a southern swell coming into Oceanside, Calif.

velocities up to 30 knots. These winds raise waves of 5–7 second-periods, 10–15 feet-heights. Such situations are likely to occur a number of times each spring, occasionally during winter and summer, but rarely during fall.

The character of the waves caused by these five meteorologic situations is summarized in Figure 7, *B*. Each rectangle shows typical height-period combinations corresponding to situations *A–E*.

LOCAL TOPOGRAPHY

The coast between Point La Jolla and the Scripps Institution pier is ideally suited for a study of changes in wave height. It is known locally that waves are usually low near the Beach Club, then increase sharply about 3,000 feet north of the Beach Club, and fall off a little in the vicinity of the Scripps Institution pier (Pl. VI). Breaker heights at different sections of this 1-mile stretch of beach generally differ by a factor of 3.

TABLE 2

	Figure No.				
	8	9	10	11	12
Wave direction	WNW	WNW	W	WNW	SSW
Wave period	14	12	12	8	16
Crest interval/period	1	1	1	2	1
Meteorological situation	A	A	A	B, C, or E	D

Such unusually large variations in breaker height can be associated with the complex submarine topography and coastline in this region. Two submarine canyons, La Jolla Canyon and its steep-walled tributary, Scripps Canyon, reach within 1,000 feet of shore (Pl. VI). These canyons have been sounded more extensively than any other submarine canyons in the world.

> The walls of La Jolla Canyon are relatively gentle except locally where slopes of 100 per cent are found. Scripps Canyon on the other hand has extremely steep walls. Numerous places have been located where the slopes are so steep that the sounding lead slides down the slope after hitting bottom. The steepest measured slope has a drop of 230 feet in a horizontal distance of 30 feet. The canyon has an inner gorge which is so narrow in places that it was difficult to locate. . . .[13]

The coast line, which is oriented NNE–SSW between Scripps pier and the Beach Club, makes an almost right-angle turn 1,000 feet south of the Beach Club and projects about 3,000 feet in a WNW direction. Point La Jolla is located at the end of this break in the coast line (Pl. VI). Beyond Point La Jolla the coast continues its NNE–SSW trend. In the vicinity of the Beach Club some protection from the usual WNW and W swell is afforded by Point La Jolla, and even more by the shoal area off this point.

REFRACTION DIAGRAMS

The refraction diagrams (Figs. 8–12) were drawn as described in the manual on breaker and surf forecasting. Table 2 gives the assumed wave direction (direction from which the wave comes in deep water), wave period, crest interval, and the corresponding meteorological situation for each of the five figures.

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[13] F. P. Shepard and K. O. Emery, "Submarine Topography off the California Coast," *Geol. Soc. Amer., Special Papers, No. 31* (May 28, 1941).

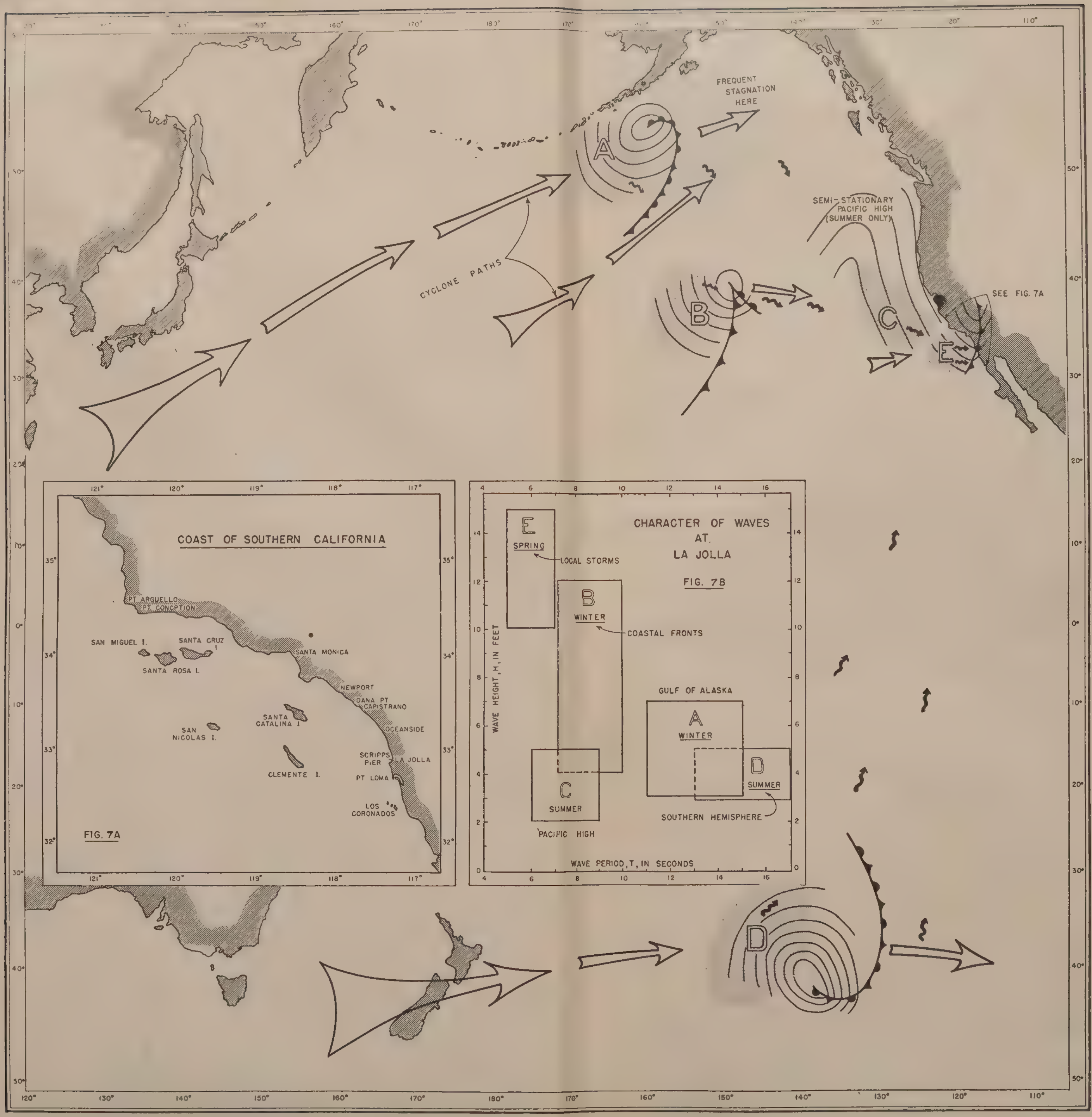
FREQUENT STAGNATION HERE
A
CYCLONE PATHS
SEMI-STATIONARY PACIFIC HIGH (SUMMER ONLY)
SEE FIG. 7A
B
C
E
D
COAST OF SOUTHERN CALIFORNIA
PT ARGUELLO
PT CONCEPTION
SAN MIGUEL I.
SANTA CRUZ I.
SANTA ROSA I.
SANTA MONICA
NEWPORT
DANA PT
CAPISTRANO
SANTA CATALINA I
SAN NICOLAS I.
OCEANSIDE
SCRIPPS PIER
LA JOLLA
CLEMENTE I.
PT LOMA
LOS CORONADOS
FIG. 7A
121° 120° 119° 118° 117°
35° 34° 33° 32°
CHARACTER OF WAVES AT LA JOLLA
FIG. 7B
E SPRING
LOCAL STORMS
B WINTER
COASTAL FRONTS
GULF OF ALASKA
A WINTER
D SUMMER
SOUTHERN HEMISPHERE
C SUMMER
PACIFIC HIGH
WAVE HEIGHT, H, IN FEET
WAVE PERIOD, T, IN SECONDS
4 6 8 10 12 14 16
0 2 4 6 8 10 12 14
120° 130° 140° 150° 160° 170° 180° 170° 160° 150° 140° 130° 120° 110°
50° 40° 30° 20° 10° 0° 10° 20° 30° 40° 50°

Fig. 7.—Origin of waves reaching La Jolla, California. The capital letters on the large chart represent typical meteorological situations, which give rise at La Jolla to waves of heights and periods shown in Figure 7, *B*. Figure 7, *A* is a chart of the region near La Jolla on an enlarged scale. The shaded areas on the large chart represent typical fetches, that is, areas where the waves are generated. The isobaric pattern and the nature of the meteorological fronts are also indicated. The large open arrows represent typical paths of the storm systems. The wavy arrows indicate the direction of the waves leaving the storm systems. The figure cannot represent the nature of the meteorological situations with any degree of accuracy but is supposed to emphasize that waves reaching La Jolla are the result of storm systems over widely separated areas of the Pacific Ocean.

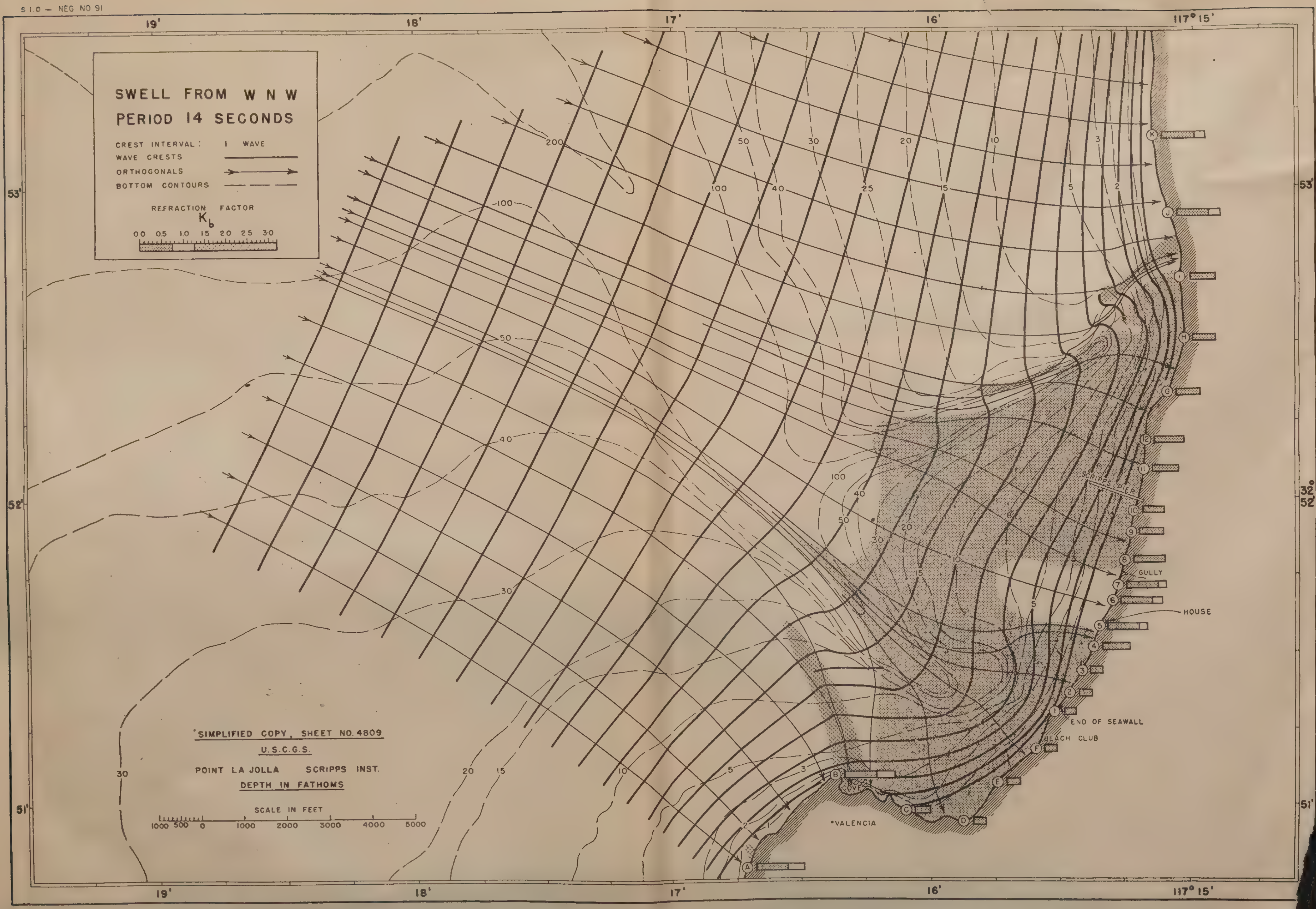
S I O — NEG NO 91
SWELL FROM W N W
PERIOD 14 SECONDS
CREST INTERVAL: 1 WAVE
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
0.0 0.5 1.0 1.5 2.0 2.5 3.0
SIMPLIFIED COPY, SHEET NO. 4809
U.S.C.G.S.
POINT LA JOLLA SCRIPPS INST.
DEPTH IN FATHOMS
SCALE IN FEET
1000 500 0 1000 2000 3000 4000 5000
19'
18'
17'
16'
117° 15'
53'
52'
32° 52'
51'
200
100
50
40
30
25
20
15
10
5
3
2
1
SCRIPPS PIER
GULLY
HOUSE
END OF SEAWALL
BEACH CLUB
COVE
VALENCIA
A
B
C
D
E
F
G
H
I
J
K
1
2
3
4
5
6
7
8
9
10
11
12

FIG. 8.—Refraction diagram for 14-second waves from the west-northwest. Heavy solid lines show positions of wave crests, the solid lines with arrowheads give orthogonals, and dashed lines are depth contours. The crosshatched re indicate zones of convergence ($K > 1.25$); the dotted regions indicate zones of divergence ($K < 0.75$). The lengths of the rectangles opposite the shore stations are proportional to K_b and thus indicate the variation of breaker heights alo beach. The general refraction pattern conforms with the schematic drawing of Fig. 3.

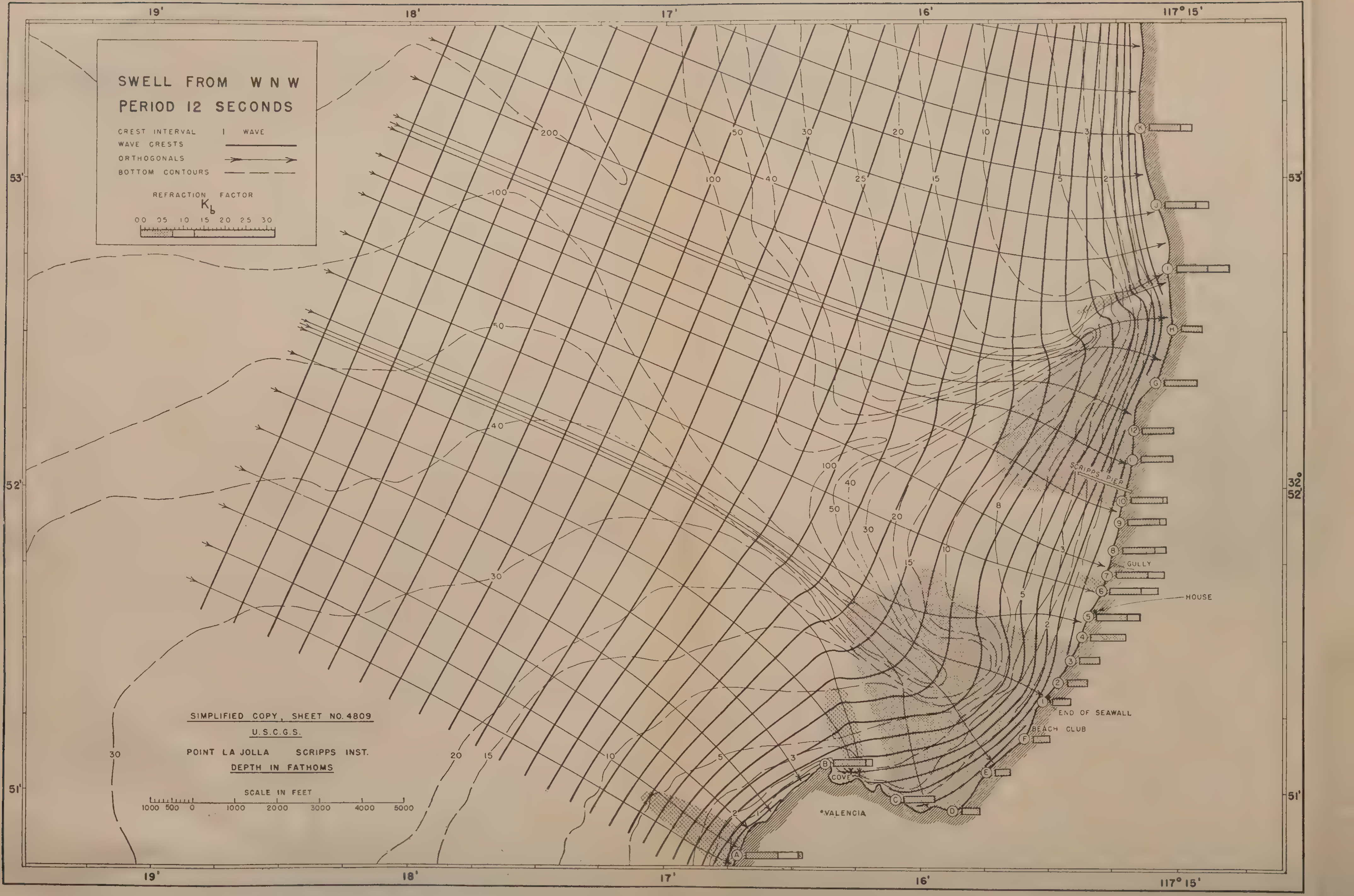
SWELL FROM W N W
PERIOD 12 SECONDS
CREST INTERVAL 1 WAVE
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
00 05 10 15 20 25 30
19'
18'
17'
16'
117° 15'
53'
52'
32° 52'
51'
200
100
50
40
30
25
20
15
10
5
3
2
1
8
SCRIPPS PIER
GULLY
HOUSE
END OF SEAWALL
BEACH CLUB
COVE
VALENCIA
A
B
C
D
E
F
G
H
I
J
K
1
2
3
4
5
6
7
8
9
10
12
SIMPLIFIED COPY, SHEET NO. 4809
U.S.C.G.S.
POINT LA JOLLA SCRIPPS INST.
DEPTH IN FATHOMS
SCALE IN FEET
1000 500 0 1000 2000 3000 4000 5000

FIG. 9.—The general refraction pattern is similar to the one in Fig. 8 but, owing to the shorter wave period, variations in wave height are smaller

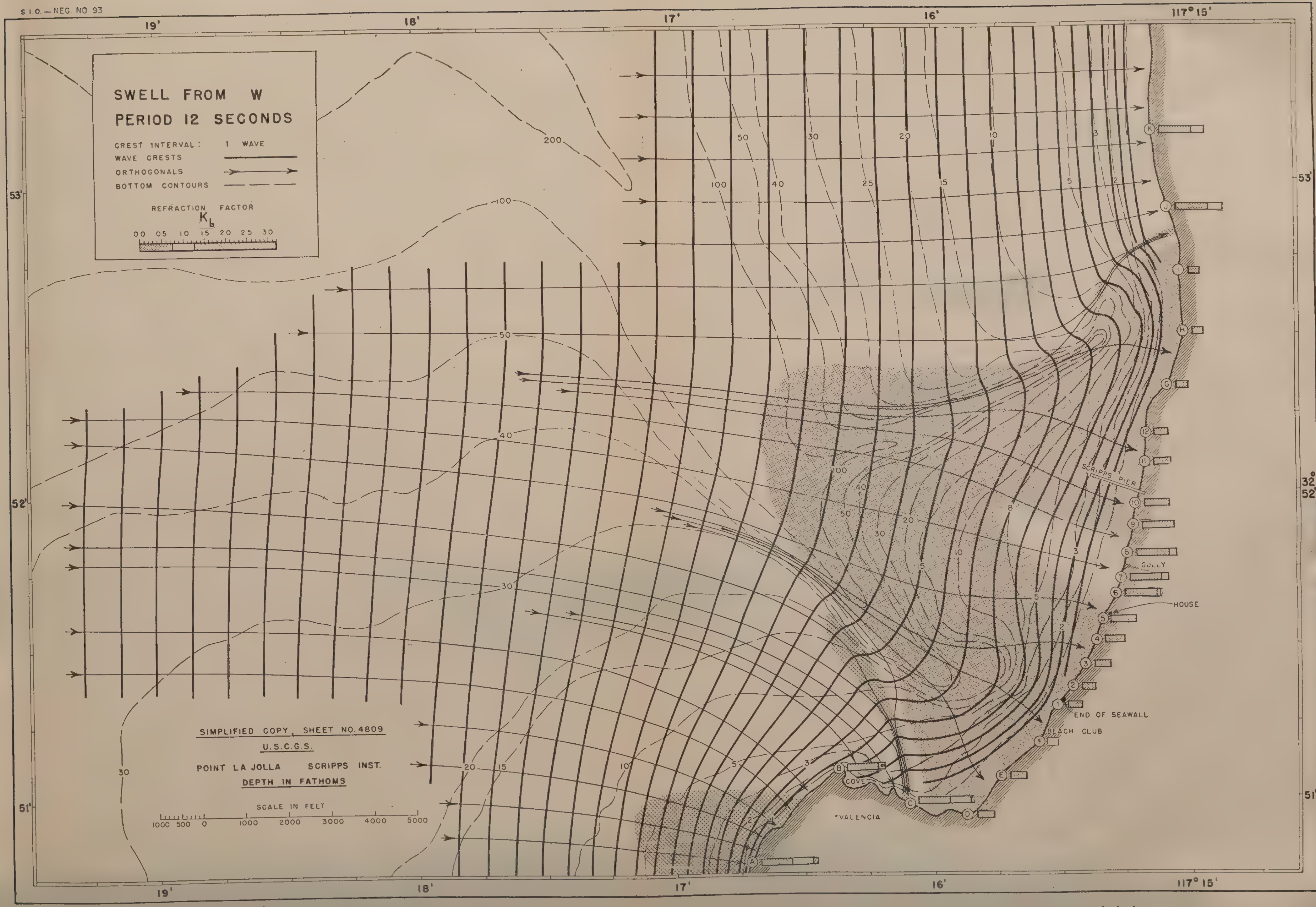
S.I.O. — NEG. NO 93
19'
18'
17'
16'
117° 15'
53'
52'
51'
32° 52'
SWELL FROM W
PERIOD 12 SECONDS
CREST INTERVAL: 1 WAVE
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
0.0 0.5 1.0 1.5 2.0 2.5 3.0
200
100
50
40
30
25
20
15
10
5
3
2
SCRIPPS PIER
GULLY
HOUSE
END OF SEAWALL
BEACH CLUB
COVE
•VALENCIA
A
B
C
D
E
F
G
H
I
J
K
1
2
3
4
5
6
7
8
9
10
11
12
SIMPLIFIED COPY, SHEET NO. 4809
U.S.C.G.S.
POINT LA JOLLA SCRIPPS INST.
DEPTH IN FATHOMS
SCALE IN FEET
1000 500 0 1000 2000 3000 4000 5000

FIG. 10.—Similar to Fig. 9, but, since the waves are assumed to come from the west rather than from the west-northwest, the entire refraction pattern is rotated counterclockwise

S I O — NEG NO 94

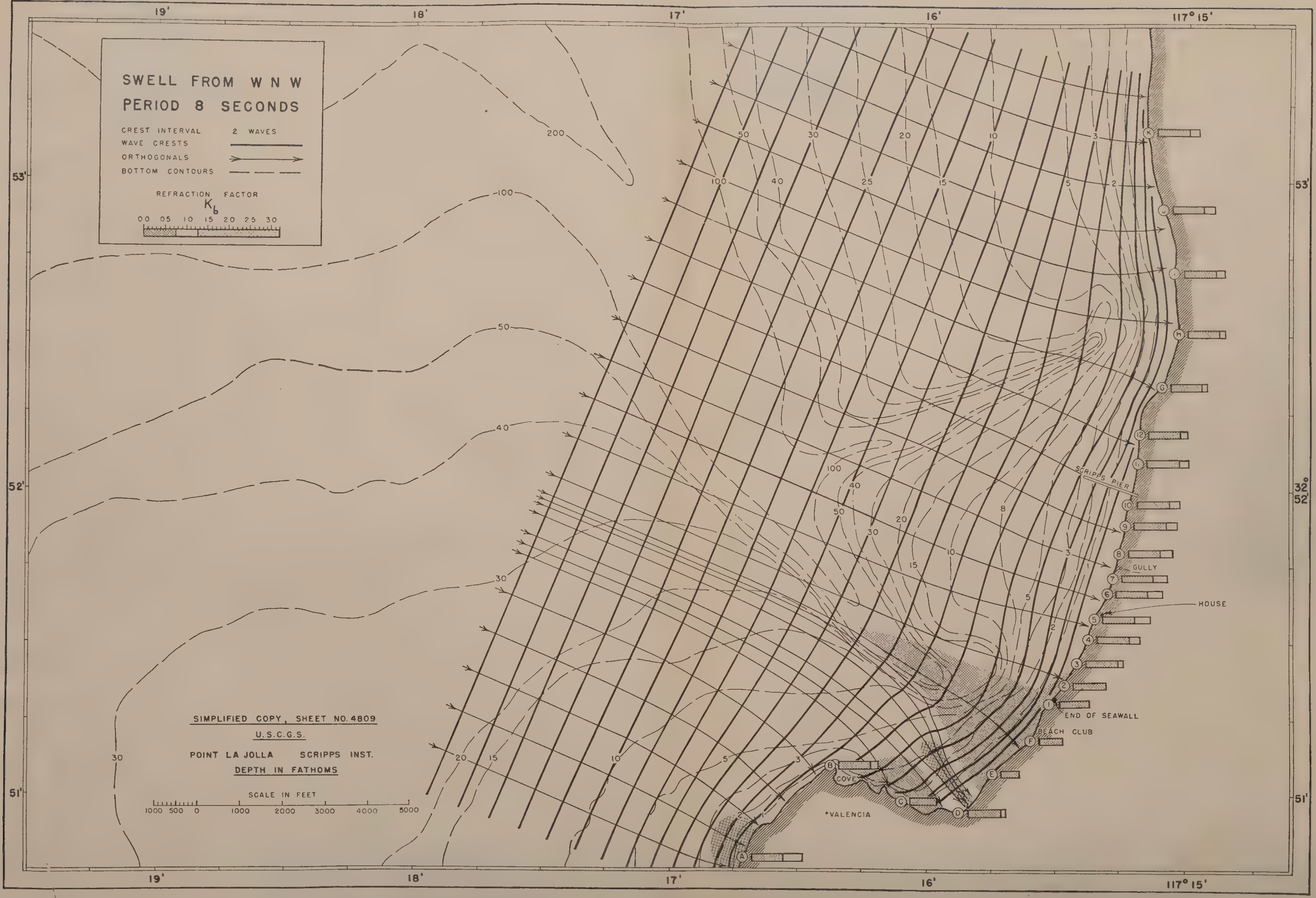
SWELL FROM W N W
PERIOD 8 SECONDS
CREST INTERVAL 2 WAVES
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
0.0 0.5 1.0 1.5 2.0 2.5 3.0
SIMPLIFIED COPY, SHEET NO. 4809
U.S.C.G.S.
POINT LA JOLLA SCRIPPS INST.
DEPTH IN FATHOMS
SCALE IN FEET
1000 500 0 1000 2000 3000 4000 5000
19'
18'
17'
16'
117° 15'
53'
32° 52'
51'
200
100
50
40
30
25
20
15
10
8
5
3
2
1
SCRIPPS PIER
GULLY
HOUSE
END OF SEAWALL
BEACH CLUB
COVE
VALENCIA
A
B
C
D
E
F
G
H
I
J
K
1
2
3
4
5
6
7
8
9
10
11
12

FIG. 11.—Owing to the short wave period, the effect of refraction is reduced even further than in the previous refraction diagrams

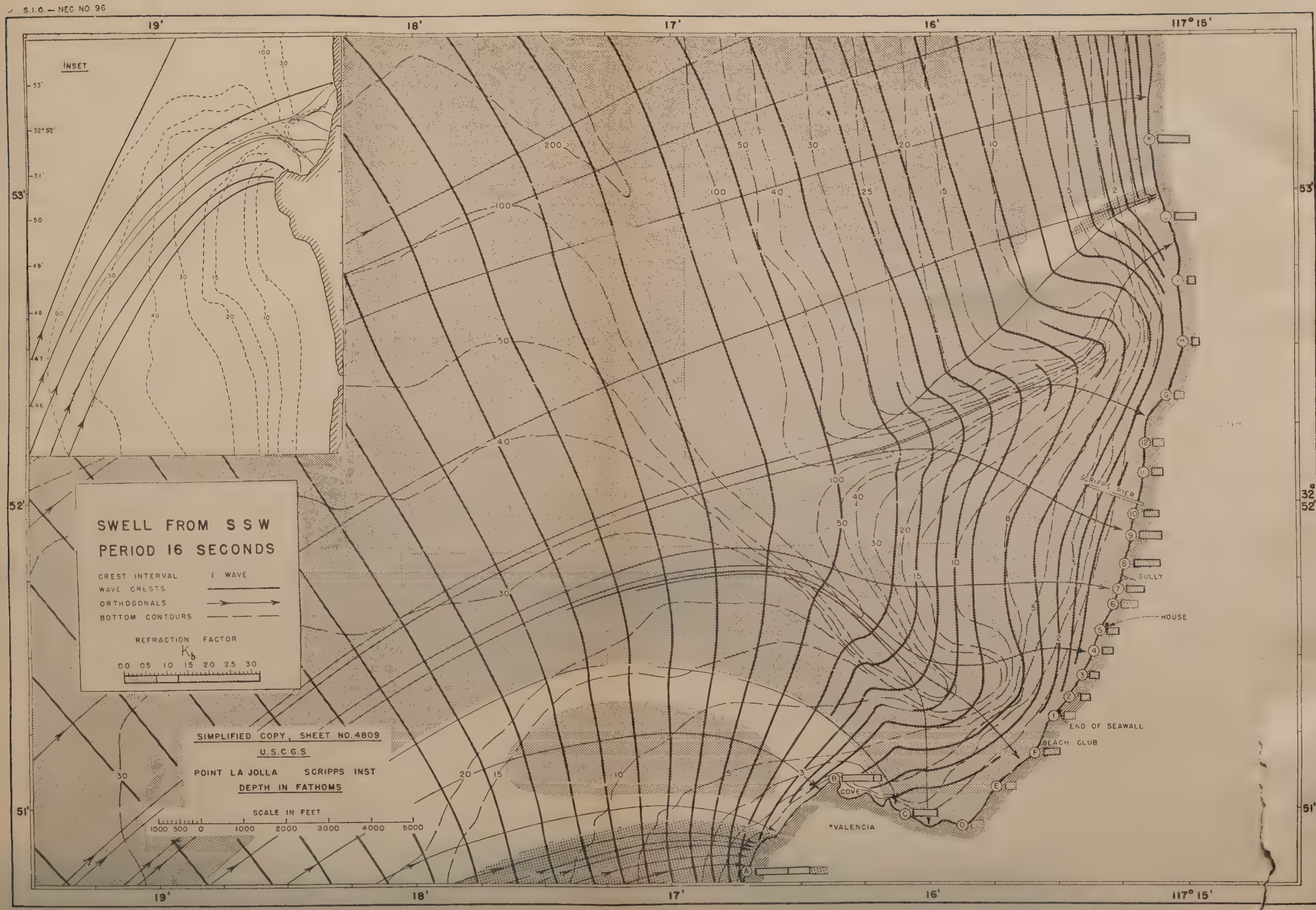
S.I.O. — NEG NO 96
19'
18'
17'
16'
117° 15'
53'
52'
32° 52'
51'
INSET
SWELL FROM S S W
PERIOD 16 SECONDS
CREST INTERVAL 1 WAVE
WAVE CRESTS
ORTHOGONALS
BOTTOM CONTOURS
REFRACTION FACTOR
K_b
0.0 0.5 1.0 1.5 2.0 2.5 3.0
SIMPLIFIED COPY, SHEET NO. 4809
U.S.C.G.S.
POINT LA JOLLA SCRIPPS INST
DEPTH IN FATHOMS
SCALE IN FEET
1000 500 0 1000 2000 3000 4000 5000
SCRIPPS PIER
GULLY
HOUSE
END OF SEAWALL
BEACH CLUB
COVE
VALENCIA
A
B
C
D
E
F
G
H
J
K
1
2
3
4
5
6
7
8
9
10
11
12
200
100
50
40
30
25
20
15
10
8
5
3
2

FIG. 12.—Except for two localities near Stations A and J, the entire area is protected from the southern swell. A few selected orthogonals between deep water and shore have been entered in an inset in order to show that for 16-second waves from the SSW the effect of refraction outside the limits of the main figure cannot be neglected.

The thin dashed lines on the figures are bottom contours in fathoms; the heavy solid lines are wave crests; and the light solid lines with arrowheads are orthogonals drawn at arbitrary intervals. For waves with periods more than 10 seconds every single crest has been drawn; for waves with periods less than 10 seconds only every second crest has been drawn.

The area offshore has been divided into divergent, normal, and convergent zones, according to whether the refraction factor K (eq. [3*a*]) is less than 0.75, 0.75–1.25 inclusive, or larger than 1.25. Divergent zones are dotted, convergent zones crosshatched, and normal zones left blank.

The value of K_b (eq. [3*b*]) at various stations is proportional to the length of the rectangles at those stations and can be read off from the scale given in the legend of each refraction diagram. In order to emphasize changes in K_b, the columns have been shaded in the same manner used for the offshore area. Columns *ending* in a dotted section designate divergence (K_b less than 0.75); those ending in a crosshatched section designate convergence (K_b larger than 1.25). It should be kept in mind that values of K are proportional to the square root and values of K_b to the cube root of the relative spacing of the orthogonals. The stations where observations were made are numbered *1–12*. Other stations, designated by the letters A–K, have been selected because of their representative location.

Waves from WNW, period 14 seconds (*Fig. 8*).—A small region of relatively high waves, or convergence, is found just north of Station A. An area of intense convergence, which extends approximately northward from the Cove (Station B), is caused by the steep south wall of La Jolla Canyon. This wall is particularly effective because it lies parallel to the direction of wave travel for half a mile. The prolonged effect of the steep bottom slope caused the waves to turn sharply to the right and converge into the Cove. This probably explains the occurrence of unusually high waves at the Cove on days when waves are low along other sectors of the beach. It is well known in La Jolla that these high waves, on days when they occur, come into the Cove at intervals of 15 minutes to several hours. Perhaps the effect of La Jolla Canyon is particularly marked for certain critical combinations of wave period and direction. Although both period and direction are nearly constant for any wave train, they do show continual small variations, and certain combinations of these periods and directions may be the cause of intermittent high waves at the Cove.

The submarine canyon offers protection along the beach from Station C to Station 5 by creating a divergence. This divergence is particularly marked in the vicinity of the Beach Club, where K_b equals 0.3. A slight convergence in the vicinity of Station 6 is the result of waves turned left by the north bank of La Jolla Canyon and is analogous to the convergence near the Cove, caused by the south bank of the canyon. The divergence between Stations 8 and I is caused by the Scripps Canyon. It is less intense than the divergence due to the La Jolla Canyon because for the direction assumed waves do not travel in a line parallel to the walls of the Scripps Canyon. To the north of the Scripps Canyon, between Stations I and J, a small but sharp convergence is found.

The variation of K_b along the beach is also shown in Figure 15. The lower portion of the figure gives the location of the stations and the two submarine canyons.

The upper figure contains a curve for K_b for each of the refraction diagrams. Low wave heights near the head of the two canyons and high waves to either side are clearly shown.

Waves from WNW, period 12 seconds (*Fig. 9*).—The general features are similar to those caused by the 14-second WNW waves, but the divergence is less intense and covers a smaller area. Wave heights between the two submarine canyons (Stations 4–9) are relatively higher than for the 14-second wave. This difference is chiefly due to the fact that the 12-second wave is shorter than the 14-second wave and that canyons and other bottom features do not affect the 12-second waves to the same degree that they affect the 14-second waves.

Waves from W, period 12 seconds (*Fig. 10*).—The main features are similar to the ones already discussed, except that regions of divergence and convergence have been shifted due to the difference of wave direction. Thus the convergence on the south edge of La Jolla Canyon has shifted from the Cove to Station C, and the convergence between the canyons from Station 6 to Station 8. The convergence near Station A is more pronounced than for a west-northwesterly swell. Scripps Canyon gives rise to more extreme divergence between Stations 11 and I because the direction of wave travel in deep water is more nearly parallel to the walls of the canyon.

Waves from WNW, period 8 seconds (*Fig. 11*).—The length of these waves in deep water is only one-third that of the 14-second swell, and the effect of refraction is reduced even more than it was for the 12-second waves. In particular, regions of divergence have become much smaller, and only about 3,000 feet of beach are protected by the La Jolla Canyon. The region of divergence opposite the Scripps Canyon has disappeared altogether. The convergence on the south side of La Jolla Canyon has moved to Station D, thus eliminating the cause of relatively high waves at or near the Cove. Nevertheless, it can be seen from Figure 15 that the refraction pattern typical of a submarine canyon has not disappeared: waves are relatively low opposite the mouth of the canyons and high on either side.

Waves from SSW, period 16 seconds (*Fig. 12*).—A few selected orthogonals between deep water and shore have been entered in an inset on a smaller scale in order to show that for this particular case the effect of refraction outside the limits of the main figure cannot be neglected. By far the larger portion of Figure 12 shows values of K less than 0.75. This divergence is due to the shoal area off Point La Jolla. At only two localities in the vicinity of La Jolla can a convergence of a southern swell be found, opposite the Casa de Mañana Hotel (Station A) and to the north between Stations J and K. A divergence followed by a convergence is caused by the ridge between the submarine canyons. It is believed that this explains the occasional occurrence of relatively high, long-period waves between Stations 7 and 9 during the summer. The refraction diagram explains also why, during the summer, waves are relatively low at the Scripps Institution while they are high at localities with southern exposure, such as near Oceanside and the Coronado Strand.

OTHER METHODS OF PRESENTING REFRACTION DIAGRAMS

If an intensive study is made of a given locality, it may be of advantage to construct a single graph from which the refraction factor K_b and the breaker angle α_b can be read off directly. In general, K_b and α_b depend upon three variables—the wave direction in deep water, the wave period, and the depth of breaking—but K_b and α_b vary slowly with the depth of breaking, and an average value for the breaking depth may be introduced.

A convenient form of presentation is a polar-coordinate graph with its center placed on an outline map at the position to which the graph applies (Fig. 13). The radial lines give the direction from which the waves come in deep water; the circles give the wave period. The solid curves are lines of equal K_b, the dashed curves lines of equal α_b. The "L = LEFT" and "R = RIGHT" refer to an observer on the beach looking straight out to sea.

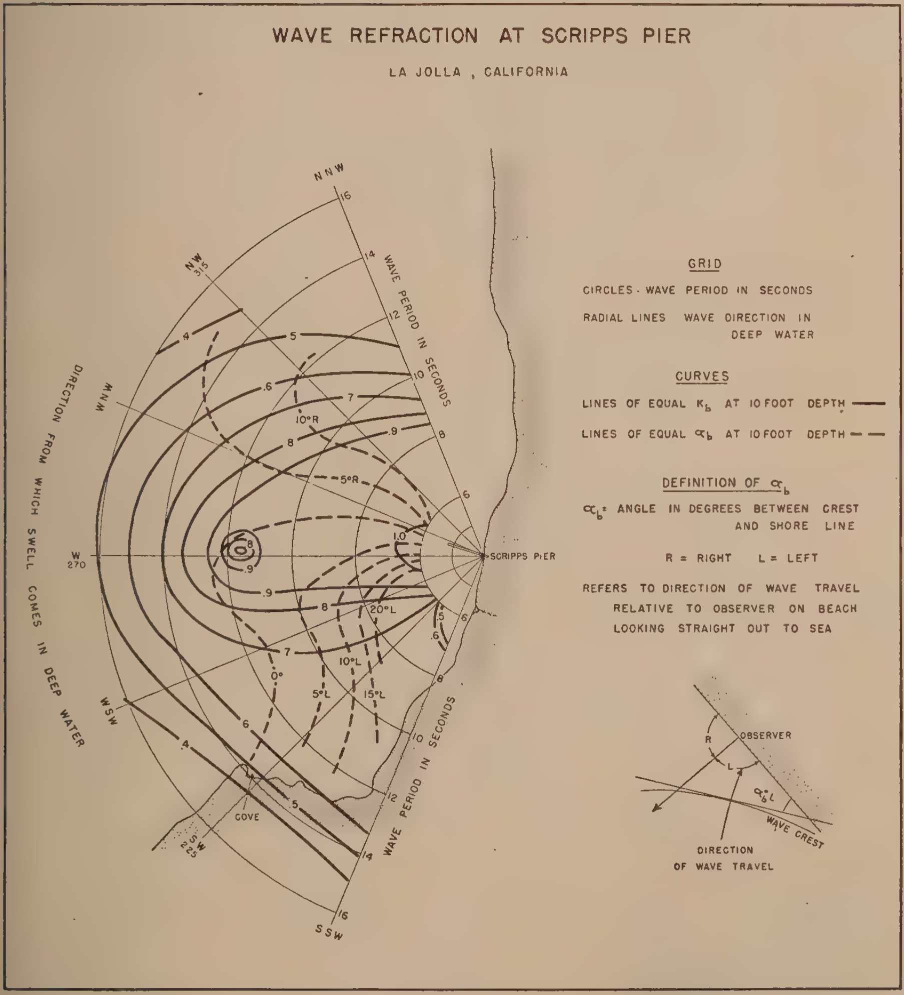

FIG. 13.—Values of K_b and α_b at a depth of 10 feet along Scripps Institution pier. The polar-coordinate presentation brings out the relative protection of the designated location from the waves coming from SSW to WSW, and the relative exposure to waves from the west.

Figure 13 is drawn for an assumed breaking depth of 10 feet along the Scripps Institution pier. The figure applies with good approximations to breakers anywhere between shore and a depth of 20 feet. The curves were drawn by interpolating between values read off Figures 8–12 and a number of other refraction diagrams drawn specially for the region in the immediate vicinity of the pier. The curve $\alpha_b = 0$ refers to breakers coming straight into shore, that is, from a WNW direction. The other dashed curves are drawn relative to this direction.

Figure 14 applies to the case of a beach with straight and parallel depth contours but is otherwise analogous to Figure 13. For this idealized case the curves for K_b and α_b are given analytically by equations (1) and (5*b*). From a comparison between Figures 13 and 14, and assuming $T = 14$ seconds, the special effects of the bottom topography and of the con-

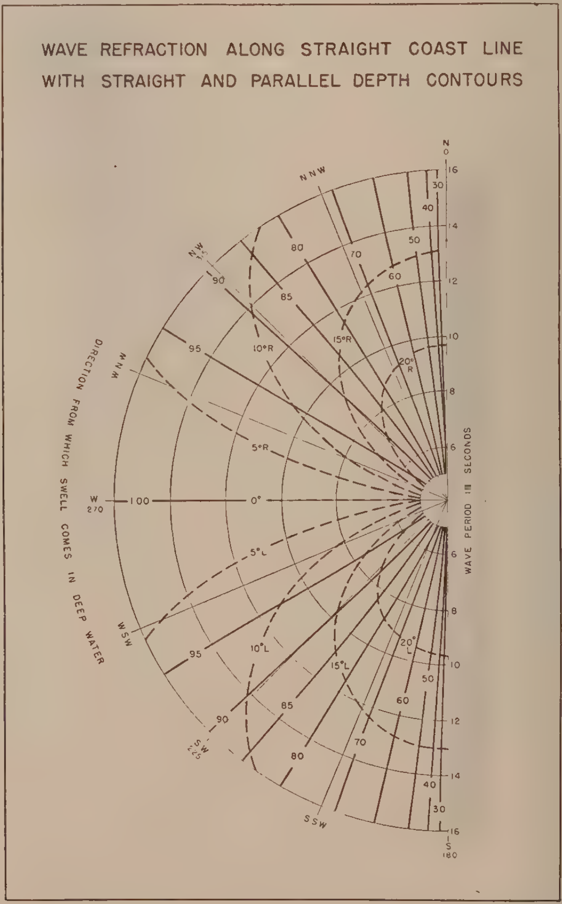
WAVE REFRACTION ALONG STRAIGHT COAST LINE WITH STRAIGHT AND PARALLEL DEPTH CONTOURS

FIG. 14.—Values of K and α_b at a depth of 10 feet for a beach with straight and parallel depth contours (eqs. [1] and [5*b*]). The special effect of the coastline and the bottom topography at La Jolla can be estimated from a comparison between Figs. 13 and 14.

figuration of the coastline upon the breakers near the Scripps pier can be evaluated (Table 3).

Thus the beach along the pier is particularly well sheltered from southerly waves due to the protection afforded by Point La Jolla and is most exposed to waves directly from the west. This type of presentation gives, therefore, an over-all picture of the protection from, or the exposure to, waves of various directions and periods. The disadvantage of this presentation is that it is limited to a relatively small area. If the emphasis is to be placed upon the changes in wave characteristics along a beach for a given wave situation, the presentation shown in Figure 15 will be more practical.

TABLE 3

	Fig.	Direction from Which Waves Come in Deep Water					
		SSW	SW	WSW	W	WNW	NW
Refraction factor K_b	13	0.51	0.45	0.57	0.70	0.60	0.45
	14	0.72	0.90	0.97	1.00	0.97	0.90
Breaker angle α_b	13	....	2°L	1°R	2°R	4°R	7°R
	14	13°L	10°L	4°L	0°	4°L	10°L

OBSERVATIONS

Naval officers under instruction at the Scripps Institution, after having been trained for one week in a uniform procedure of observing waves, occupied Stations 1–12 along the beach and made simultaneous observations for 15 minutes. These observations were averaged to obtain observed values. To minimize differences due to personal judgment, observers were shifted regularly from one station to another. From about seventy complete sets of observations, 7 days were selected during which the swell period was well defined and in agreement with forecasts. According to forecasts, all these waves came from WNW. Observations are summarized in Table 4. For each of the twelve stations Table 4 gives the height of the breakers in feet, the height of the breakers as percentage of the average for all stations, and the wave period in seconds. The value for H_b at Station 6 on January 5 appears to be too high, but otherwise observations are fairly consistent.

For each *station* observations made on the 7 days under consideration were averaged and entered in the last column of Table 4. For each *day* observations made at the twelve stations were averaged and entered at the bottom of the table, together with the forecast values. On the 7 days under consideration the average periods vary between 11.5 and 13.8 seconds. The over-all average for observed periods is 12.5 seconds, and for the forecast periods 14 seconds. The forecast direction is WNW. Figures 8 and 9 should therefore apply in all seven cases.

COMPARISON OF THEORY AND OBSERVATIONS

The *computed* refraction factor K_b for waves of 14- and 12-second periods from the WNW was read off at each of the twelve stations. In the case of the 14-second wave, the average value for all stations was 0.62; in the case of the 12-second wave, 0.82. At each station the individual values of K_b were then expressed as percentages of these average values and plotted in Figure 16 (solid and dashed curves).

The dots in Figure 16 give the average *observed* breaker height and the crosses the average *observed* wave periods, both expressed as percentages of the over-all average for all days and stations. These values were taken from the last column of Table 4. In view of the inaccuracies of the observations and the difficulty in drawing exact refraction diagrams, the agreement between theory and observation is satisfactory. The only noticeable discrepancy occurs near Station 7, where the computed wave height exceeds the observed height by about 10 per cent. This discrepancy may be related to a shifting sand bank about 2,500 feet south of the pier.

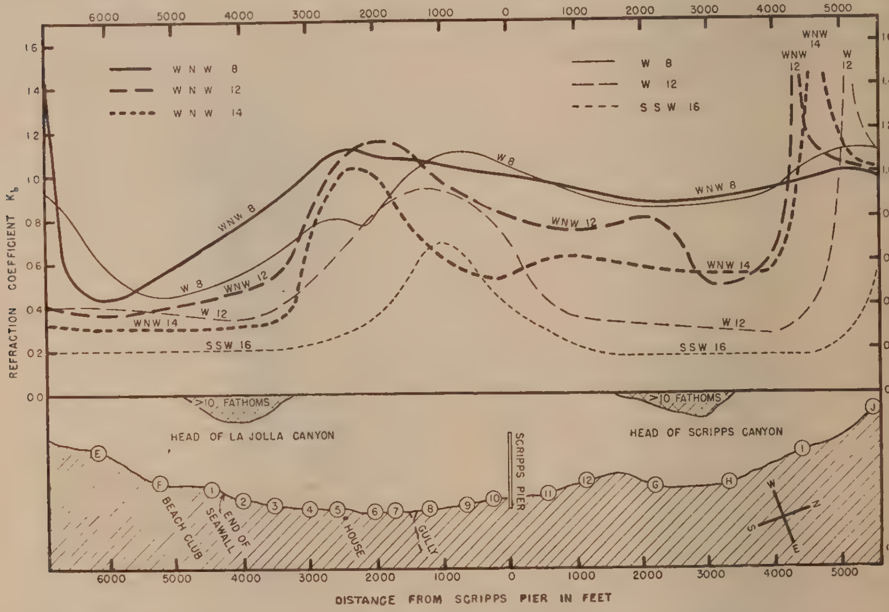

FIG. 15.—Variations of K_b along the coastline according to the refraction diagrams. The lower section of the figure shows the locations along the beach to which values of K_b in the upper section refer. For all but the southern swell, waves are generally lower near the head of the canyon than on either side. Short wave periods give smaller variations in wave height than longer periods. Changes in wave direction shift the location of the zones of convergence and divergence, but they have little effect upon the amplitude of the variation in K_b.

According to theory, the wave periods should remain constant. Observations plotted in Figure 16 show that this is nearly the case, the lowest value being 95, and the highest 105, per cent of the average. It happens that these small variations in period are in phase with the variations in wave height.

The refraction diagrams can also be compared directly to aerial photographs. Plate VII was selected for an example, because it shows an unusually regular, well-defined swell. The area covered in the photograph extends between Station 5 and Station G.

The swell shown on the photograph was generated in a low-pressure area

TABLE 4

OBSERVATIONS OF BREAKER HEIGHT AND PERIOD

STA. NO.	DEC. 1, 1944			DEC. 8, 1944			JAN. 2, 1945			JAN. 3, 1945			JAN. 5, 1945			FEB. 13, 1945			FEB. 14, 1945			PER CENT AVERAGES	
	H_b		T (Sec.)	H_b		T (Sec.)	H_b		T (Sec.)	H_b		T (Sec.)	H_b		T (Sec.)	H_b		T (Sec.)	H_b		T (Sec.)	H_b	T
	Ft.	%		Ft.	%		Ft.	%		Ft.	%		Ft.	%		Ft.	%		Ft.	%			
1	0.7	33	11.5	2.0	38	11	1.0	45	.....	1.0	34	14.0	1.0	22	12.0	3.0	75	12.0	1.5	50	10.0	42	95
2	1.3	62	12.0	2.0	38	11	1.0	45	14.5	1.0	34	11.0	1.5	33	14.0	2.5	63	12.0	2.0	67	9.0	49	94
3	1.5	71	12.0	.....	.....	.....	2.5	114	12.0	1.5	52	13.5	2.0	44	14.0	1.8	45	14.0	3.0	100	12.0	71	102
4	1.5	71	12.0	5.5	104	12	2.5	114	14.0	3.5	121	11.0	4.0	87	12.0	5.0	125	12.0	3.0	100	12.0	103	97
5	2.5	119	13.0	6.0	113	12	3.0	137	14.0	5.0	173	14.0	6.0	130	14.5	6.0	150	13.0	4.0	133	12.0	136	105
6	3.5	167	12.0	4.5	85	12	3.5	159	14.5	4.0	138	14.0	11.0	240	16.0	4.5	113	12.0	4.0	133	11.0	148	103
7	3.5	167	12.0	5.0	94	13	2.5	114	14.0	4.0	138	15.0	5.0	109	15.0	5.0	125	12.0	3.5	117	11.0	123	104
8	3.0	143	12.0	6.0	113	12	2.0	91	13.0	2.5	86	10.0	4.5	98	13.0	4.0	100	12.5	3.5	117	14.0	107	99
9	2.5	119	13.0	6.5	123	13	2.5	114	13.0	3.5	121	11.0	4.5	98	13.0	3.5	88	11.5	3.5	117	11.5	111	98
10	1.5	71	13.0	8.0	151	10	.....	.....	.....	3.5	121	12.0	.....	.....	.....	4.0	100	11.5	3.0	100	11.0	100	95
11	1.5	71	13.0	6.5	123	11	2.0	91	14.0	2.5	86	12.0	5.0	109	12.0	4.0	100	12.0	3.0	100	13.0	97	99
12	.....	.....	.....	6.0	113	13	2.0	91	14.5	2.5	86	14.0	6.0	130	14.0	5.0	125	12.0	2.5	83	11.0	105	103
Av.	2.1	100	12.2	5.3	100	11.7	2.2	100	13.8	2.9	100	12.8	4.6	100	13.6	4.0	100	12.2	3.0	100	11.5	100	12.5
Forecast	3.6	(WNW)	13.0	5.8	(WNW)	12.0	2.0	(WNW)	14.0	2.4	(WNW)	15.0	3.0	(WNW)	15.0	2.6	(WNW)	14.0	3.8	(WNW)	14.0	.....	14.0

1,700 miles WNW of San Diego. The wind blew at 35 knots over a fetch of 800 miles. This situation persisted without much change from May 1 to May 3, 1944. Applying the forecasting method,[14] one obtains 6-foot breakers of 15.5-second period near the Scripps Institution pier at the time the photograph was taken. The height and period, computed from the photograph according to the method given in the surf forecasting manual,[15] equal 7 feet and 14 seconds, respectively. The breaker characteristics computed from weather maps agree with those obtained from the photograph, and the refraction diagram for 14-second waves from the WNW (Fig. 8), should be applicable.

A comparison between Figure 8 and Plate VII shows good agreement between the orientation and spacing of computed and photographed crests. To

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[14] "Wind Waves and Swell, Principles in Forecasting," *Hydrographic Office, U.S. Navy, Misc. 11275* (1944). Cf. ftn. 2.

[15] Pp. 42–52 of ftn. 2.

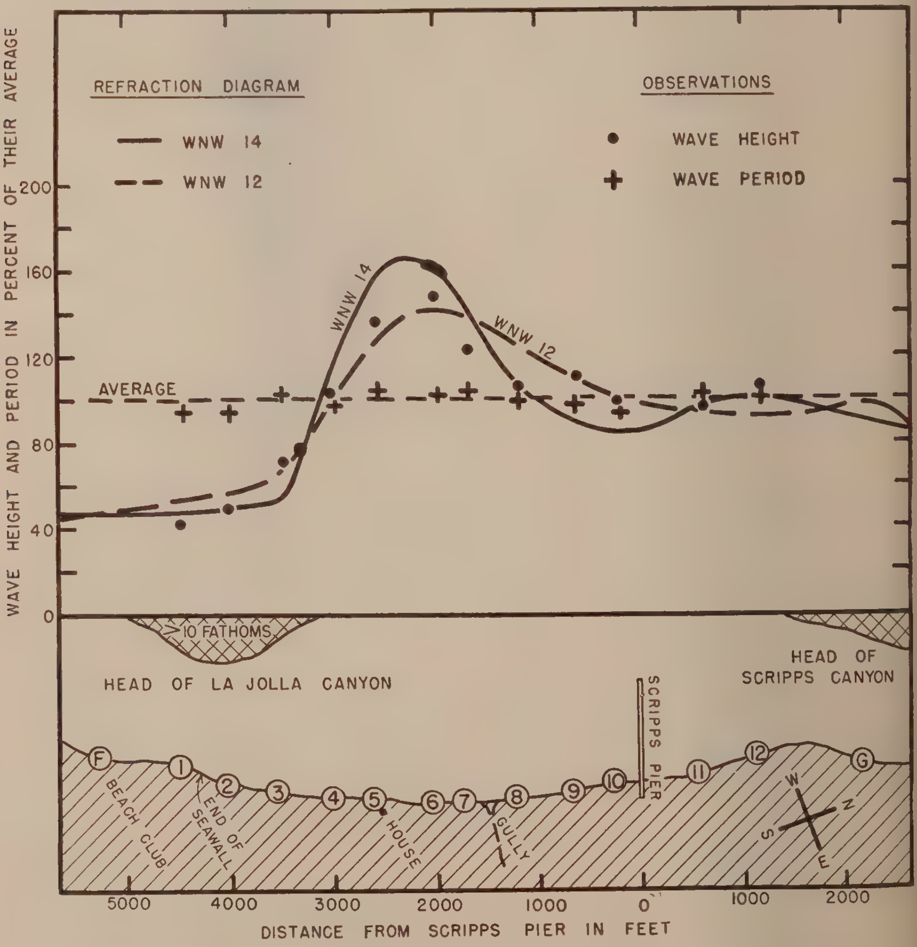
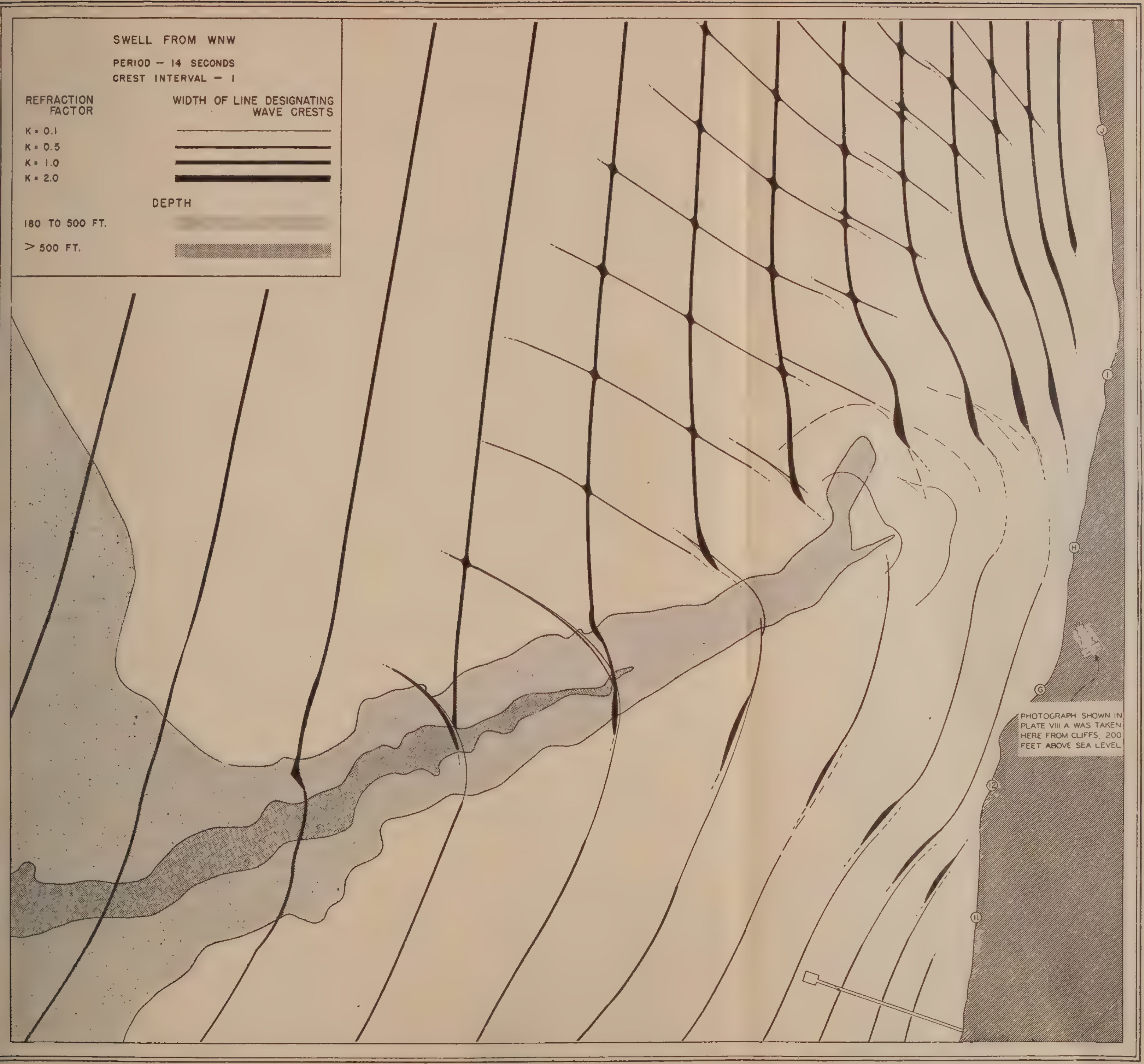


FIG. 16.—Observed versus computed changes in wave height along the beach (see text)


SWELL FROM WNW
PERIOD — 14 SECONDS
CREST INTERVAL — 1
REFRACTION FACTOR
WIDTH OF LINE DESIGNATING WAVE CRESTS
K = 0.1
K = 0.5
K = 1.0
K = 2.0
DEPTH
180 TO 500 FT.
> 500 FT.
J
I
H
G
12
11

PHOTOGRAPH SHOWN IN PLATE VIII A WAS TAKEN HERE FROM CLIFFS, 200 FEET ABOVE SEA LEVEL

Fig. 17.—Detailed refraction diagram of waves over Scripps Canyon. The shaded areas denote depths exceeding 180 feet, and 500 feet, respectively. The degree of convergence nd divergence is indicated by the width of the lines designating wave crests. The figure illustrates how steep bottom features can break up a simple wave train into a omplex pattern.

facilitate the comparison, some of the crests have been transferred from Figure 8 to Plate VII, where they are shown by the inked lines. Near the left edge of Plate VII the photographed crests lag, indicating a shallow bank. On a photograph taken 5 months later a similar lag occurred about 500 feet farther south. This evidence indicates the existence of a shifting sand ridge. The depth contours on Figure 8, which are based on soundings taken prior to 1928, cannot take into account such temporary features. It is quite possible that the discrepancy between observed and computed wave heights near Station 7 is also related to this shifting sand bank.

CROSSING OF WAVE TRAINS NORTH OF SCRIPPS CANYON

At the time the refraction diagrams (Figs. 8–12) were drawn, it was expected that they could give only the basic features regarding the positions of crests and the variations in wave height. Accordingly, small-scale features in the bottom topography and sharp bends in the crests or orthogonals were smoothed out, and the smoothed crest was used as a basis for the construction of the next crest. This crest was also smoothed, when necessary, and this smoothing process was continued from crest to crest as the waves were carried toward shore. In this manner a cumulative error is introduced into the refraction diagram.

If these diagrams are drawn with greater precision, and without smoothing, it is found that the steep walls on the northern side of Scripps Canyon cause a section of the crest to be bent through 90°. This section will travel north along the coast and intersect the regular wave train in a crisscross pattern.

The crisscross pattern is illustrated in Figure 17, which shows a large-scale graph of the refraction of 14-second waves from the WNW over Scripps Canyon between Stations 12 and J. The outermost crest has been transferred from Figure 8. The remaining crests were carried forward with a crest interval of one-eighth the wave period and without smoothing, but only one out of eight computed crest positions is shown on the figure (crest interval = one period). The actual construction of the refraction diagram was carried out on a detailed chart, but only two depth contours are shown on the figure.

It should be kept in mind that the shading in Figure 17 designates bottom topography and not convergence or divergence. In order to picture the degree of divergence or convergence, the *width* of the crest lines has been drawn proportional to the refraction factor K according to the scale in the legend. Wherever the refracted crests intersect the main wave train, a hump on the sea surface is formed, the height of which equals the sum of the height of the two intersecting waves.

Plate VIII, *A*, shows a photograph of this wave pattern, taken from the top of the cliffs at a position indicated on Figure 17. The wave crests in the photograph have been slightly retouched to make them appear more clearly in print. The pattern on the photograph resembles closely the pattern on the refraction diagram.

DISCUSSION AND CONCLUSIONS

METEOROLOGY AND WAVE REFRACTION

In order to draw a refraction diagram, it is necessary to know (1) the wave period and direction in deep water and (2) the bottom topography between deep water and the shoreline. The determination of typical wave periods and deep-water directions for a given locality will be discussed first, and the bottom topography and its effect will be taken up in the following section.

In the experience of the authors, existing observational data on wave characteristics are almost always inadequate for determining typical deep-water wave directions and periods for a given locality. Data on deep-water wave direction are usually lacking entirely, because they require the services of a boat or a plane. Wave period, since it remains constant, can be measured from shore, but the methods of measuring have been for the most part inconsistent and inadequate.

A better procedure is to obtain the wave characteristics from a knowledge of meteorological conditions and the relationships between wind, sea, and swell.[16] Weather maps are examined to determine all wind areas where waves affecting the locality of interest could be generated. The characteristics of the waves upon reaching the given locality are then computed by the relationships mentioned.

This method has been employed in a study for the United States Navy of the effect of wave conditions upon seaplanes. Meteorologists at the Scripps Institution carried out a day-by-day "forecast" for specified localities on the basis of historical weather maps,[17] the forecasts extending over 3 years. This method required considerable work and highly trained personnel. Fortunately, only a small number of localities have to be considered, since offshore conditions are sufficiently uniform to make the computed wave conditions applicable over long stretches of coastline.

The procedure described above consists essentially of computing wave characteristics from *synoptic* weather data and then applying statistical methods to the computed wave data for deriving *climatological* wave conditions. In this report a somewhat less accurate procedure has been followed by making use of average wind data obtained from climatological charts for the different seasons. An exceptionally complete set of wave observations at La Jolla, dating back to 1938, has made it possible to check the soundness of this procedure. Even so, it has been necessary to depend entirely upon local observations for information regarding the southern swell which originates in an area of the South Pacific for which weather data are lacking.

BOTTOM TOPOGRAPHY AND WAVE REFRACTION

Detailed hydrographic charts are required for an accurate construction of refraction diagrams. However, the main features in the refraction pattern can be associated with certain types of underwater topography without the need of elaborate computations (Figs. 1–6 and Pls. I–V). Quite generally it can be shown that the wave refraction pattern for any bottom topography follows a single law, according to which **waves change direction and are bent in such a manner that they *tend* to assume the shape of the depth contours.** Thus the wave crests on an aerial photograph draw a quasi-depth chart. This circumstance has found application during the war in determining underwater topography over enemy beaches.

Associated with the distortion of the waves are local convergences and divergences of wave energy. It is important to make a distinction between an area of *divergence* and what might be called a complete wave *shadow zone*. Waves behind a headland or to the lee of an island are usually very low because of the divergence of wave energy, yet the protected region does not lie in a wave shadow zone. Indeed, sensitive instruments have shown that waves can reach any section of a coastline, no matter how well protected, unless that section is completely cut off from communication with the open sea. By the time the waves have turned through a large angle, they are usually too low to be noticeable to the naked eye, but in some instances local convergences in so-called protected zones have led to surprising results.[18]

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[16] See ftn. 7.

[17] A complete set of Northern Hemisphere weather maps, dating back to 1929, were prepared during the war under the auspices of the Joint Meteorological Committee of the Army, Navy, and Weather Bureau.

THE CONCEPT OF RELATIVE DEPTH

It should be emphasized that the effect of bottom features upon waves depends not upon the absolute depth of water but upon the *relative depth*, that is, the ratio of depth over deep-water wave length (h/L_0). Let h and L_0 be given in feet, and the wave period T in seconds. Setting $g = 32.2$ ft/sec² in Appendix equations (A5*b*) and (A6*a*), one obtains approximately $L_0 = 5\,T^2$, and

$$\text{Relative depth: } \frac{h}{L_0} = \frac{h}{5T^2}. \qquad (6)$$

By definition shallow water has a relative depth of less than one-half. For a long 14-second swell shallow water starts therefore at a depth of 500 feet; for a short 7-second wind wave, at 125 feet. Since modification of waves occurs only in shallow water, a shoal at an average depth of 500 feet would affect the swell in a manner similar to that in which a shoal at 125 feet would affect the short-period sea. An interesting application of this principle is the *separation* of a short-period sea from a long-period swell by special types of bottom features. The bottom topography itself can be compared to an enormous lens, separating waves of different frequencies much as a lens breaks up light into the component colors. A famous illustration of this feature is provided by the surf at Waikiki beach in the Hawaiian Islands, which usually results from a NE swell refracting around Nakapuu Point and Diamond Head. Out at sea a short NE chop will usually be present in addition to the swell, but the chop is too short to be refracted effectively and thus passes on without bending into the beach.

Since ordinary waves rarely have periods much longer than 14 seconds, the effect of underwater bathymetry on these waves is virtually limited to the continental shelf. But sea and swell are not the only waves of the sea refracted by the ocean bottom. Fault movements associated with submarine earthquakes generate very long waves, "tsunamis," popularly called tidal waves (although they are not related to tides), and these have periods ranging between 10 minutes and an hour. In accordance with equation (6), these waves are always in shallow water, even over the deepest portion of the oceans. Preliminary results of an investigation by Shepard and others[19] show a good correlation between the variations in the height of the April, 1946, tsunami in the Hawaiian Islands and the offshore topography and promise an interesting application of the principles discussed in this paper. A similar effect, but of even larger order of magnitude, must result from the refraction of tsunamis by large-scale bathymetric features, such as ocean basins and troughs. This might explain the curious fact that waves of the April, 1946, tsunami were recorded about twice as high at South American stations as they were at stations along California, although they had originated near the Aleutian trough and traveled more than twice as far to the South American stations.

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[18] An interesting application of the effect of refraction on wave height was made in connection with the liberation of the Philippine Islands. During the planning stage refraction diagrams were prepared for waves entering the Lingayen Gulf from the north, and they showed a convergence for the landing beaches, but a divergence east of the town of Lingayen. Consequently, an alternate plan was made to provide for the contingency of high waves from a typhoon. Shortly after the initial landings, high breakers prevented unloading at the main beachhead, but the breakers remained low to the east of Lingayen as indicated on the refraction diagram. A second beachhead was established according to the alternate plan, and the unloading of supplies continued without interruption.

[19] G. A. MacDonald, F. P. Shepard, and D. C. Cox, "The Tsunami of April 1, 1946, in the Hawaiian Islands (Preliminary Report)," *Pacific Sci.*, Vol. I No. 1 (January, 1947), pp. 21–37.

WAVE REFRACTION AND BEACH EROSION

Krumbein[20] in his study of Half Moon Bay, California, was probably the first to consider the effect of wave refraction on sediment transport. He states that a refraction diagram indicated at least the order of change in wave energy along the coast. In the present paper it is shown that refraction diagrams also give this change quantitatively. This conclusion is of particular significance because the unusually complex bottom topography off La Jolla provides a critical test of the application of refraction theory to ocean waves. It also appears that wave refraction can be depended upon to give not only the simple main features regarding wave height and direction but also more complicated secondary effects, such as the crisscross pattern north of Scripps Canyon.

Refraction diagrams, if properly used, can become a powerful tool in the study of beach erosion. Although several processes are involved, two must be of particular importance in the effect of refraction upon beach erosion: (1) transport of sediments by *advection* associated with the secondary current system set up by the waves and (2) transport of sediments by *diffusion* associated with the turbulence set up by the breakers. The former process depends critically upon the *direction* of the waves, the latter upon the variation in *height* of the waves. The two processes depend, therefore, upon the two elements of the refraction pattern.

The term "advection" has been borrowed from meteorology or oceanography, where it denotes a transport due to a current flowing from a region of high concentration to a region of low concentration. Mathematically the effects of diffusion and convection are both contained in the vector equation

$$\frac{\partial s}{\partial t} = \nabla^2 \cdot \mathbf{A} - \nabla \cdot s\mathbf{V}\,, \tag{7}$$

where s is any concentration, **A** the vector coefficient of kinematic eddy diffusivity, and **V**, the vector velocity. Equation (7) states that the local time change of any concentration equals the effect of diffusion minus the effect of advection. For further discussion refer to chapter v of Sverdrup *et al.*[21]

Of the currents set up by the waves, the most important are probably longshore currents, or littoral currents, and rip currents.[22] The longshore currents are set up by the transport of waves breaking at an angle with the shoreline. They are directed, therefore, *with* the longshore component of the wave motion—for example, from left to right in Figure 1. In the case of high waves and breakers forming an angle of more than 10° with the coastline, longshore currents may attain velocities of several knots. If it were not for the fact that breaker angles are greatly reduced by refraction, longshore currents would attain such high velocities that the rate of beach erosion would be many times its actual value.

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[20] "Shore Processes and Beach Characteristics," *Technical Memorandum No. 3, Beach Erosion Board* (May, 1944).

[21] H. U. Sverdrup, M. W. Johnson, and R. H. Fleming, *The Oceans, Their Physics, Chemistry and General Biology* (New York: Prentice-Hall, 1942).

[22] F. P. Shepard, K. O. Emery, and E. C. La Fond, "Rip Currents: A Process of Geological Importance," *Jour. Geol.*, Vol. XLIX, No. 4 (May–June, 1941), pp. 337–69.

The refraction pattern for submarine canyons causes the longshore currents to diverge from the center of the canyon toward both sides, leading to a removal of sediment from the canyon head. In the case of submarine ridges, the longshore currents and the sediments converge upon the ridge. Submarine canyons and ridges are associated, therefore, with a refraction pattern which sets up a current system that tends to perpetuate their existence.

Rip currents are directed from shore out to sea. Along a straight coastline they are most pronounced when the waves come straight toward shore. Usually the location of rip currents is closely associated with the refraction pattern. In the case of submarine canyons, rip currents tend to form at the zones of convergence at either side of the canyon, although frequently they turn and flow directly over the canyon just outside the breaker zone. In the case of ridges, rip currents tend to form in the convergence above the ridges. Exceptions to all these rules are, however, frequently found. The effectiveness of rip currents in transporting sand can be gauged by the fact that they have been observed to erode a channel several feet deep within a short time interval.[23]

Transportation of sediments by *diffusion* must result from the variation of wave heights along the beach. Wave heights are low opposite the mouth of the submarine canyons and high on either side. Since high breakers cause a heavy degree of turbulence, and low breakers only little turbulence, sand may be kept in suspension on the sides of the canyons while it has a chance to settle over the canyon. In the case of submarine ridges similar reasoning leads to the conclusion that the ridges tend to be eliminated by diffusion. Thus the effect of diffusion is opposite to the effect of advection. Since it is known that the heads of submarine canyons are kept fairly clean of sediments[24] and that ridges may exist for long times, it appears that the advective processes must balance the effects of diffusion and slumping.

Tidal currents are rarely of much importance along open coastlines exposed to severe wave action. The change in tide level may, however, be important, since it causes a back-and-forth shift of the surf zone, which in turn will have an effect upon the location of longshore currents, rip currents, and the zones of maximum turbulence. The rise and fall of the mean sea-level makes it impossible for any beach ever to reach a state of complete equilibrium.

It should be emphasized that the manner in which sediment is transported by wave action is not properly understood and that many exceptions have been found to the foregoing statements. Conditions, as they exist along a beach at any given time, approach a sensitive balance between erosion and deposition. The balance is profoundly disturbed by any changes in the wave and weather conditions or by the building of jetties and breakwaters. For similar reasons the manner in which the sands along a beach are shifted back and forth by wave action must depend greatly upon the refraction pattern. The resulting sediment transport may cause changes in depth which in turn affect the refraction pattern (Pl. VIII, *B*). This interplay between waves and bottom makes the prediction of changes in the bottom profiles extremely difficult. But by analyzing the effects of wave action from the point of view of fluid mechanics, making use also of refraction diagrams, it seems likely that a better understanding of the processes involved in beach erosion will result.

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[23] *Ibid.*, pp. 350–52.

[24] Shepard and Emery, pp. 94–103 of ftn. 13.

Another point of view we have tried to introduce into this report is the importance of meteorology to studies of beach erosion. A season which is unusual from the point of view of beach conditions must, in the final analysis, be the result of unusual meteorological conditions over the ocean. This does not necessarily mean that local weather conditions have been unseasonal. We have noted, for example, that some of the swell reaching southern California in the summer depends upon weather conditions in the Southern Hemisphere, perhaps 5,000 miles away. The ever changing beaches along the shorelines are a reflection of the infinite number of possible combinations and variations of storms over widely spread areas of the ocean.

APPENDIX

THEORY OF WAVE REFRACTION

Let E denote the mean energy per unit surface area, n the fraction of this energy advancing with the wave crest at velocity C, and s the distance between adjacent orthogonals. Then, if energy is conserved between orthogonals,

$$E_0 n_0 C_0 s_0 = EnC s = E_b n_b C_b s_b \,, \qquad \text{(A1)}$$

where the subscript "o" refers to deep-water conditions, i.e., water whose depth exceeds one-half the wave length, and the subscript b to the breaker point. The expression without subscripts holds generally in shallow water, intermediary between deep water and the breaking-point.

In deep water the wave energy is proportional to the *square* of the wave height H_0 according to the equation

$$E_0 = \tfrac{1}{8}\rho g H_0^2 \,, \qquad \text{(A2}\,a\text{)}$$

where ρ is density and g the acceleration due to gravity. The same relationship holds with good approximation in shallow water:

$$E = \tfrac{1}{8}\rho g H^2 \,. \qquad \text{(A2}\,b\text{)}$$

However, just outside the breaking-point, the shape of the waves approaches that of "solitary waves," with sharp isolated crests, separated by long flat troughs. For solitary waves the wave energy is proportional to the cube of the wave height, according to the equation

$$E_b = \frac{\rho g}{L_b}\left(\frac{4h_b H_b}{3}\right)^{3/2} . \qquad \text{(A2}\,c\text{)}$$

Combining the first two expressions of equations (A1) and (A2), we get the following general relationship for the wave height in shallow water:

$$\frac{H}{H_0} = \left(\frac{n}{n_0}\,\frac{C}{C_0}\,\frac{s}{s_0}\right)^{-1/2} . \qquad \text{(A3)}$$

In deep water only half the energy, the potential energy, advances with the wave form:[25]

$$n_0 = \tfrac{1}{2} \,. \qquad \text{(A4}\,a\text{)}$$

In the breaker zone both potential and kinetic energy travel with the waves,

$$n_b = 1 \,, \qquad \text{(A4}\,b\text{)}$$

while for shallow water in general

$$n = \frac{1}{2}\left[1 + \frac{\dfrac{4\pi h}{L}}{\sinh\left(\dfrac{4\pi h}{L}\right)}\right] . \qquad \text{(A4}\,c\text{)}$$

Equation (A4*c*) reduces properly to equations (A4*a*) or (A4*b*), depending upon whether the ratio h/L has a large or small value.

The velocity of sinusoidal irrational waves of low amplitude is given by the classical Stokes's equation

$$C^2 = \frac{gL}{2\pi}\tanh\frac{2\pi h}{L} \,, \qquad \text{(A5}\,a\text{)}$$

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[25] H. U. Sverdrup and W. H. Munk, "Wind, Sea and Swell: Theory of Relations for Forecasting," *Hydrographic Office, Technical Report in Oceanography No. 1* (in press).

hich for deep water reduces to the form

$$C_0^2 = \frac{gL_0}{2\pi}. \qquad \text{(A5}\,b\text{)}$$

Since wave period T, defined as the ratio of ave length over wave velocity, remains onstant

$$T = \frac{L_0}{C_0} = \frac{L}{C} = \frac{L_b}{C_b} \qquad \text{(A6}\,a\text{)}$$

r

$$\frac{C}{C_0} = \frac{L}{L_0}. \qquad \text{(A6}\,b\text{)}$$

Dividing (A5*a*) by (A5*b*) and making use of A6*b*), we get

$$\frac{C}{C_0} = \frac{L}{L_0} = \tanh\frac{2\pi h}{L}. \qquad \text{(A7)}$$

quation (A7) can also be written

$$\frac{L}{L_0} = \tanh\left[2\pi\frac{h}{L_0}\left(\frac{L}{L_0}\right)^{-1}\right], \qquad \text{(A7}'\text{)}$$

hich is an equation of the form

$$\frac{L}{L_0} = \text{function}\left(\frac{h}{L_0}\right). \qquad \text{(A8)}$$

he ratio h/L_0 is termed "relative depth." It ollows from equations (A7) and (A8) that the atio C/C_0 is a function of the relative depth nly. In a similar manner it can be shown that he ratio n/n_0 is a function of the relative depth.

Thus equation (A3), which can be written

$$\frac{H}{H_0} = \left(\frac{n}{n_0}\frac{C}{C_0}\right)^{-1/2}\sqrt{\frac{s_0}{s}}, \qquad \text{(A9)}$$

onsists of two parts: the first part, which deends upon the relative depth and does not ontribute toward a *variation* in wave height long any fixed contour, and the second part, e refraction factor, according to which any ariation in wave height along a beach outside e breaker zone, must be proportional to the quare root of s_0/s.

To find the corresponding expression for the reakers, combine the first and third term of quations (A1) and (A2)

$$\frac{C_0}{2}\,\frac{1}{8}H_0^2 s_0 = \frac{C_b}{L_b}\left(\frac{4h_bH_b}{3}\right)^{3/2} s_b,$$

where use has been made of equations (A4*a*) and (A4*b*). In view of (A6*a*), this can be written

$$h_bH_b = \tfrac{3}{4}\left(\tfrac{1}{16}\right)^{2/3}\left(H_0^2L_0\right)^{2/3}\left(\frac{s_0}{s_b}\right)^{2/3}. \qquad \text{(A10)}$$

According to theory substantiated by experiments with solitary waves,

$$h_b = 1.28H_b, \qquad \text{(A11)}$$

and equation (A10) becomes

$$\frac{H_b}{H_0} = \frac{1}{3.3\sqrt[3]{\frac{H_0}{L_0}}}\sqrt[3]{\frac{s_0}{s}}. \qquad \text{(A12)}$$

Any *variation* in breaker height must be proportional to the cube root of s_0/s. The ratio H_0/L_0 is called the wave steepness in deep water. Equation (A12) and the foregoing discussion hold strictly only for waves of steepness H_0/L_0 less than 1 per cent (i.e., for swell) but is approximately true for all but the steepest storm waves.

The general equation (A9) for wave heights in shallow water neglecting refraction was first derived by Green in 1839 and extended by O'Brien and Mason[26] to include the refraction effect. The existence of solitary waves was first noticed by Russell, and their theory was developed by Boussinesque in his study of tide waves and related phenomena. The application of the solitary-wave theory to surf problems and the derivation of equation (A12) are believed to be new.

Acknowledgments.—We are indebted to Dr. H. U. Sverdrup for the active role he has played in developing the theory and application of wave refraction. Dr. F. P. Shepard and Mr. D. Leipper have made many helpful suggestions. The exacting job of constructing the refraction diagrams in Figures 8–12 was undertaken by Sgt. R. Jentoft, AC, while on duty at the Scripps Institution. Mr. D. Pritchard has drawn the complex refraction diagram shown in Figure 17.

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[26] Pp. 37–39 of ftn. 5.

PLATE I

A, Long waves from the southern hemisphere approaching the coast north of Oceanside, California. Compare refraction pattern with schematic drawing in Fig. 1. (Official photograph, United States Navy.)

B, Refraction of waves over ridge along the northern shore of Oahu, T.H. (cf. Fig. 4). Over the ridge waves lag behind and are higher than on either side. (Official photograph, United States Army.)

PLATE II

Refraction of waves over submarine canyon at Redondo, California (cf. Fig. 3). Waves bend sharply forward over canyon. Waves are higher just outside the canyon than over the canyon, and the surf zone is narrow opposite the mouth of the canyon. (Photograph by Spence Air Photos, Los Angeles.)

PLATE III

Refraction of waves over the coral reef at Guam. Wave crests move ahead over the channels and lag behind over the shoals. Wave heights are low over channels and large over shoals. Compare with schematic drawings in Figs. 3 and 4. (Official photograph, United States Navy.)

PLATE IV

A, Refraction of waves around Point Loma, San Diego, California. Solid orthogonal shows main refraction around the point; dashed orthogonal designates secondary refraction around a shoal directly off the end of Point Loma. Notice variation in width of surf zone. (Official photograph, United States Navy.)

B, Waves turn through 180° around the hook of Cape Cod but, in doing so, lose most of their height because of the very large divergence. Notice variation in width of surf zone. (Official photograph, United States Navy.)

PLATE V

Waves bend toward the famous Waikiki Beach on Oahu, T.H. (Official photograph, United States Navy.)

PLATE VI

Photograph of a three-dimensional model of the bottom topography off La Jolla, California. Two submarine canyons, La Jolla Canyon and its steep-walled tributary, Scripps Canyon, reach within a thousand feet from shore.

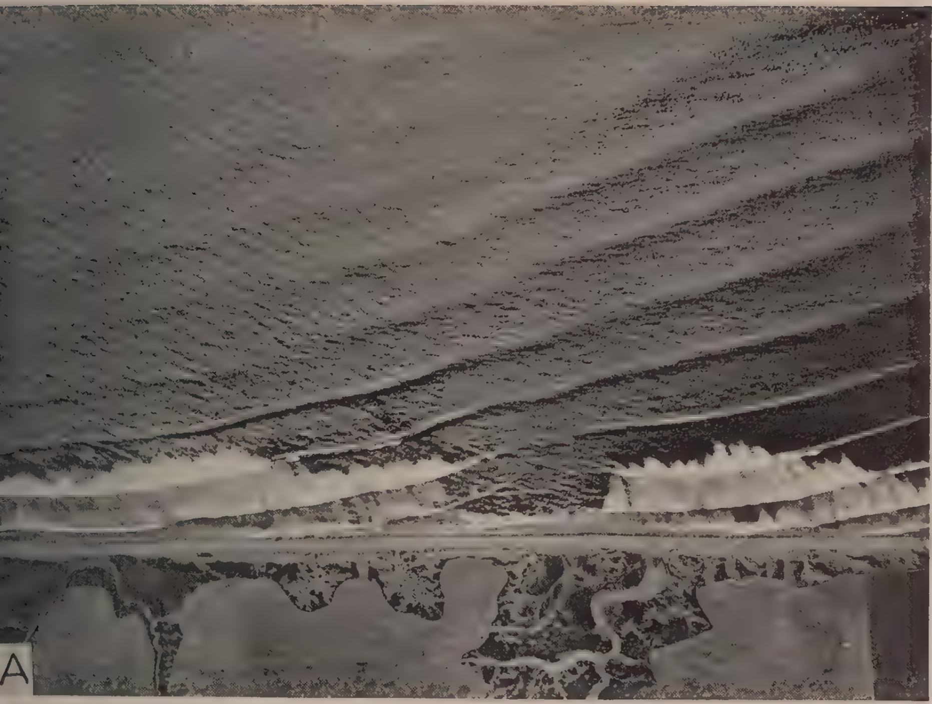
PLATE VII

Observed versus computed orientation and spacing of wave crests. The computed positions (*inked lines*) are parallel to the positions of the crests on the photograph, except for a small discrepancy on the left side of the figure (see text).

PLATE VIII

A, Photograph of waves north of Scripps Canyon shows the presence of the crisscross pattern which appears in the refraction diagram (Fig. 17). Peaks occur where the refracted crests intersect the crests of the main wave train.

B, Refraction of waves at boat basin, Oceanside, California. Longshore currents set up by waves have widened the beach on both sides of jetties (see also Pl. II). This in turn has caused refraction of waves near jetties. The resulting refraction pattern tends to further strengthen the convergence of longshore currents upon the jetties and may lead to accelerated deposition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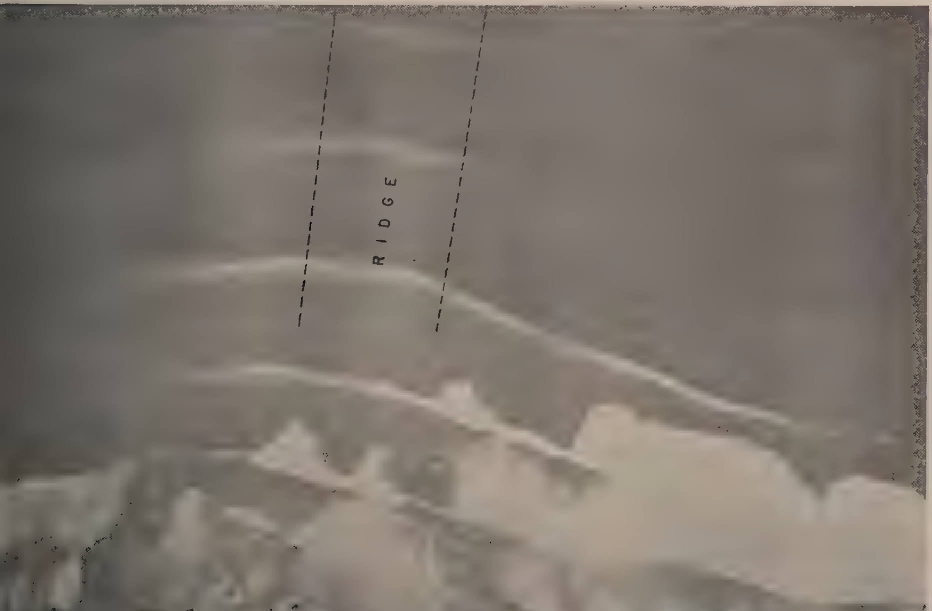

RIDGE
B

PLATE II

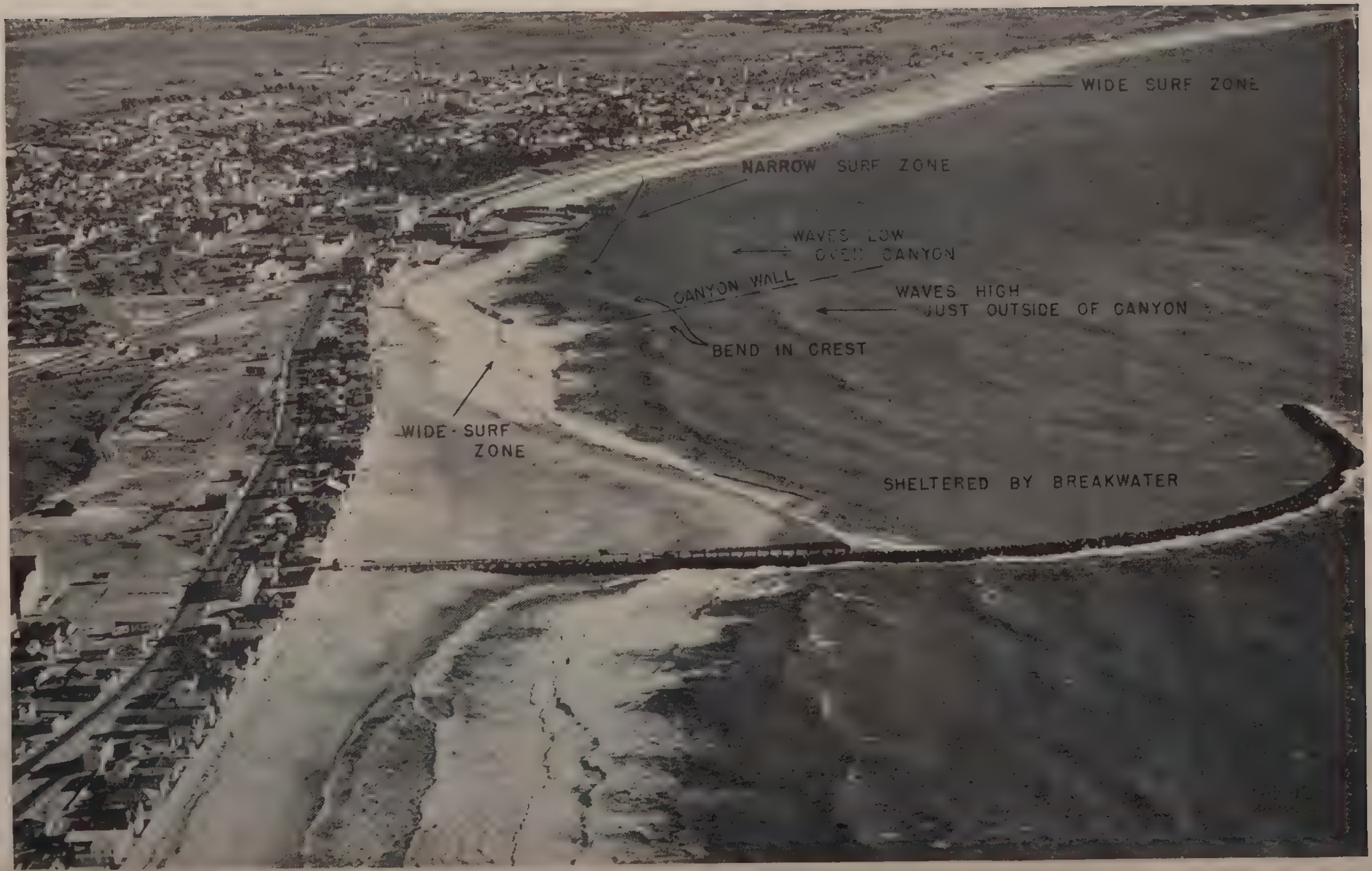

WIDE SURF ZONE
NARROW SURF ZONE
WAVES LOW OVER CANYON
CANYON WALL
WAVES HIGH JUST OUTSIDE OF CANYON
BEND IN CREST
WIDE SURF ZONE
SHELTERED BY BREAKWATER

PLATE III

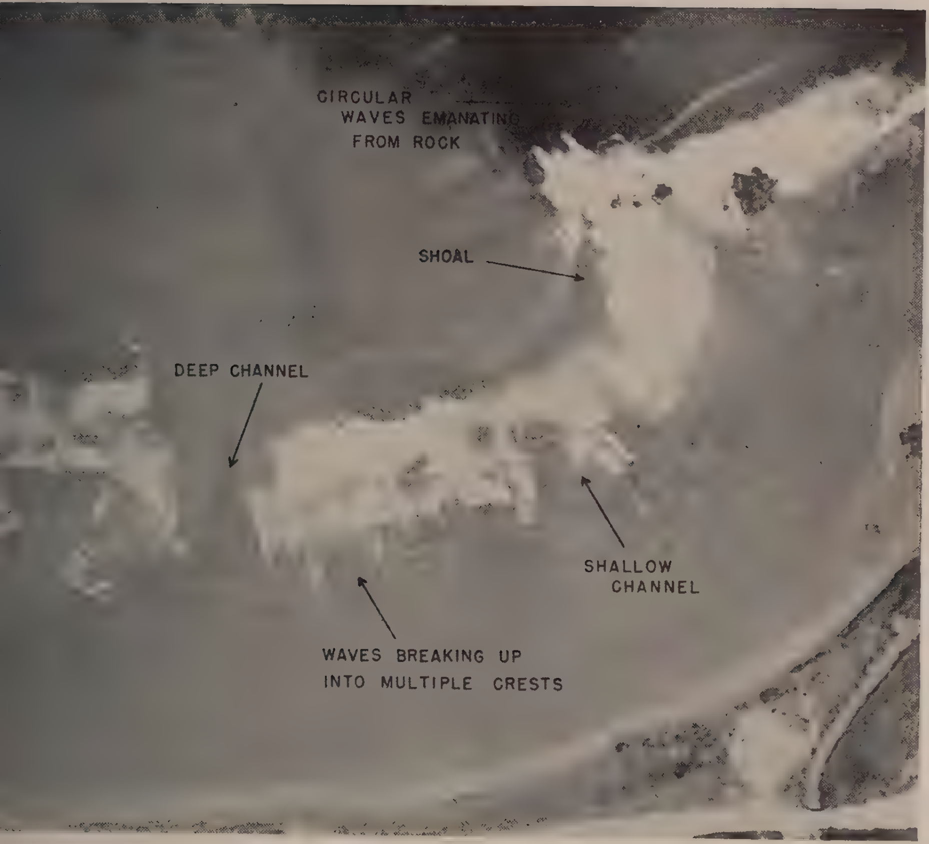
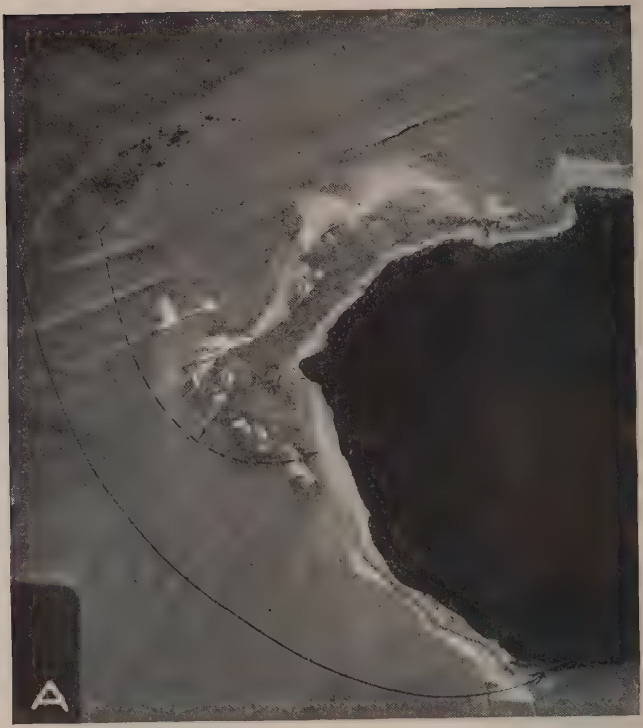

CIRCULAR
WAVES EMANATING
FROM ROCK
SHOAL
DEEP CHANNEL
SHALLOW
CHANNEL
WAVES BREAKING UP
INTO MULTIPLE CRESTS

PLATE IV



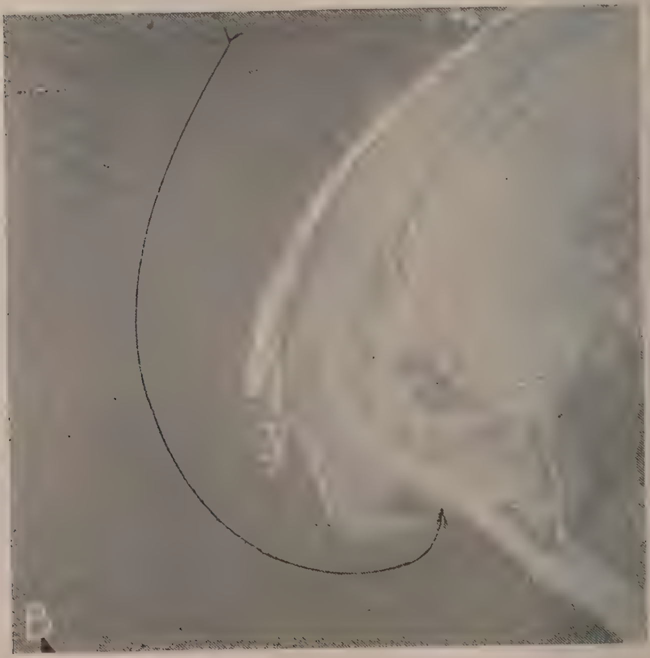
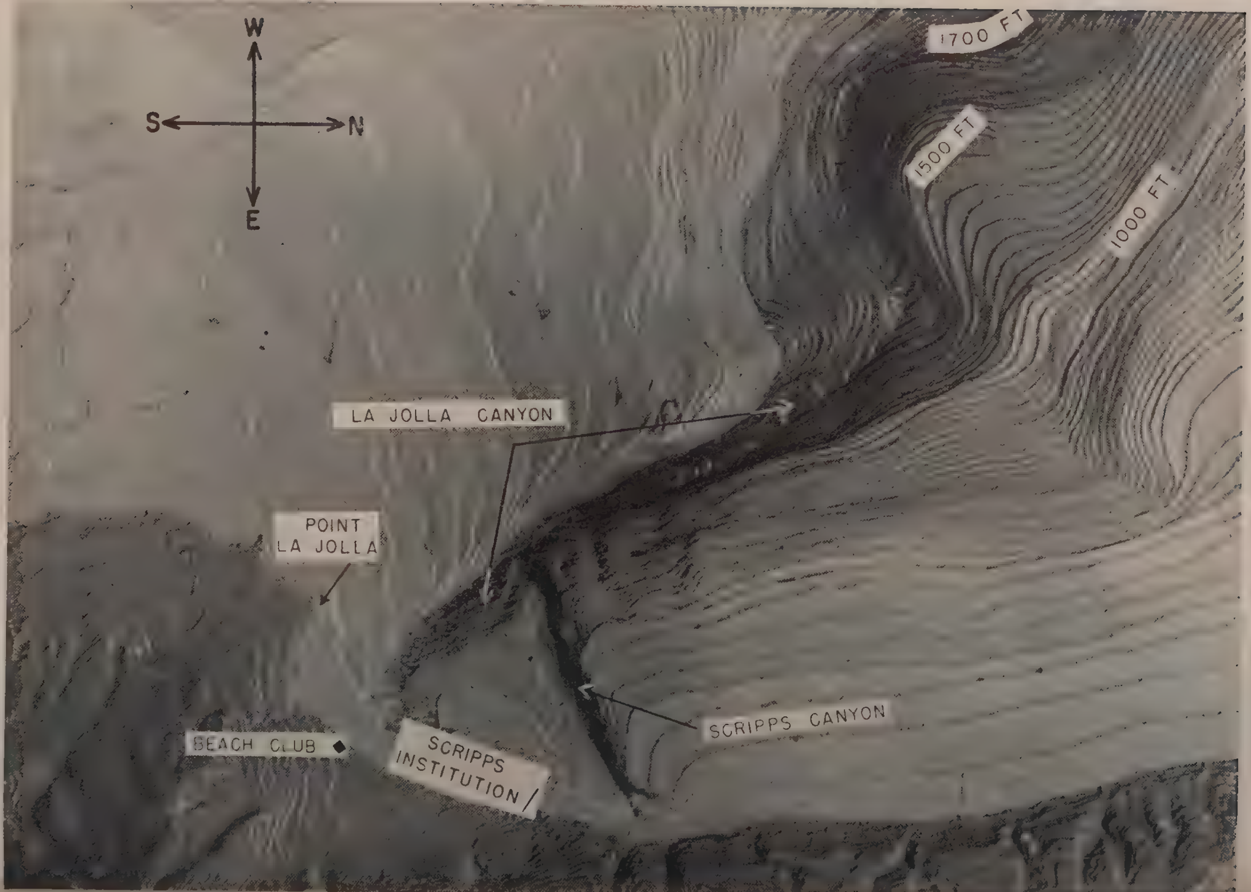


PLATE VI



W
S
N
E
1700 FT
1500 FT
1000 FT
LA JOLLA CANYON
POINT
LA JOLLA
SCRIPPS CANYON
BEACH CLUB
SCRIPPS
INSTITUTION

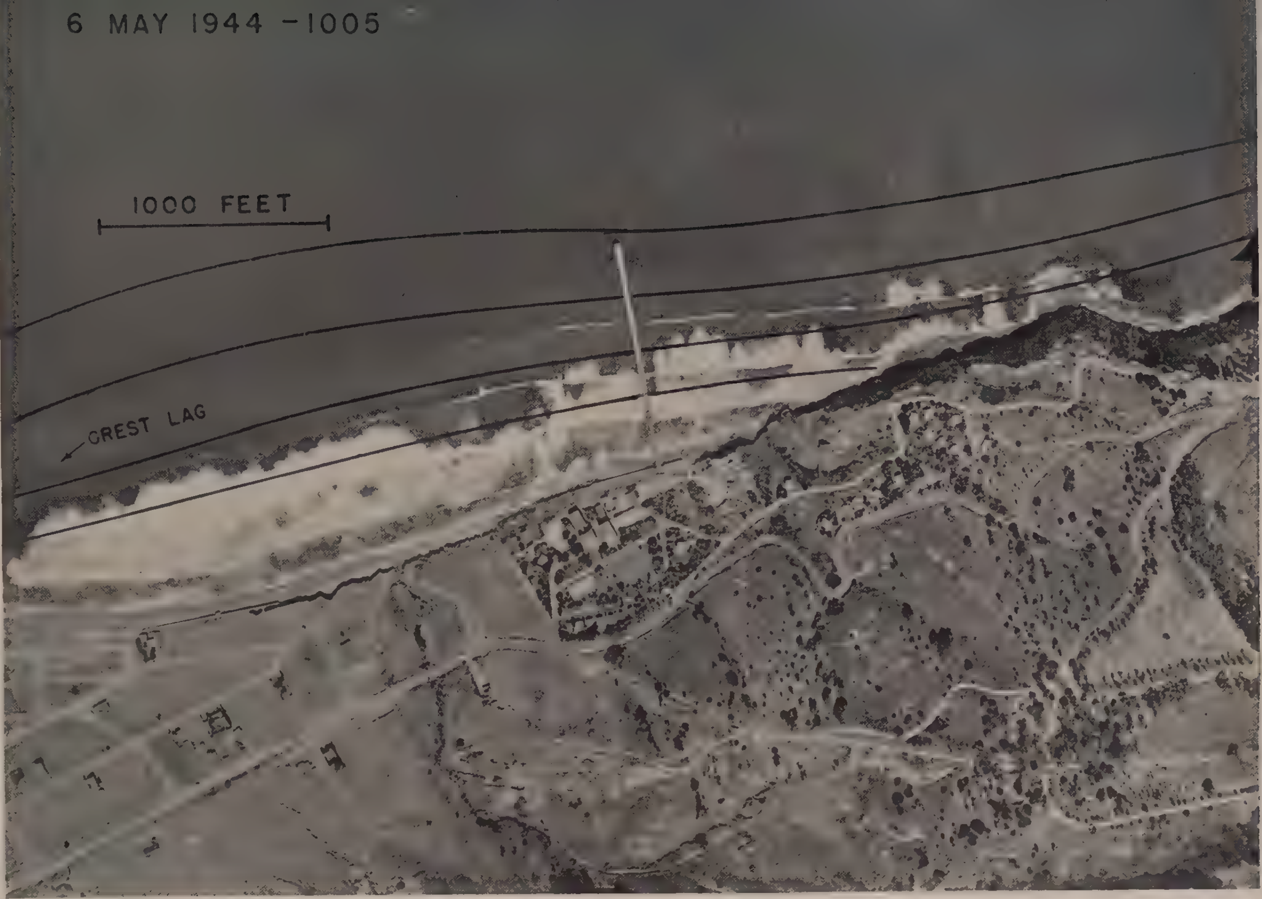
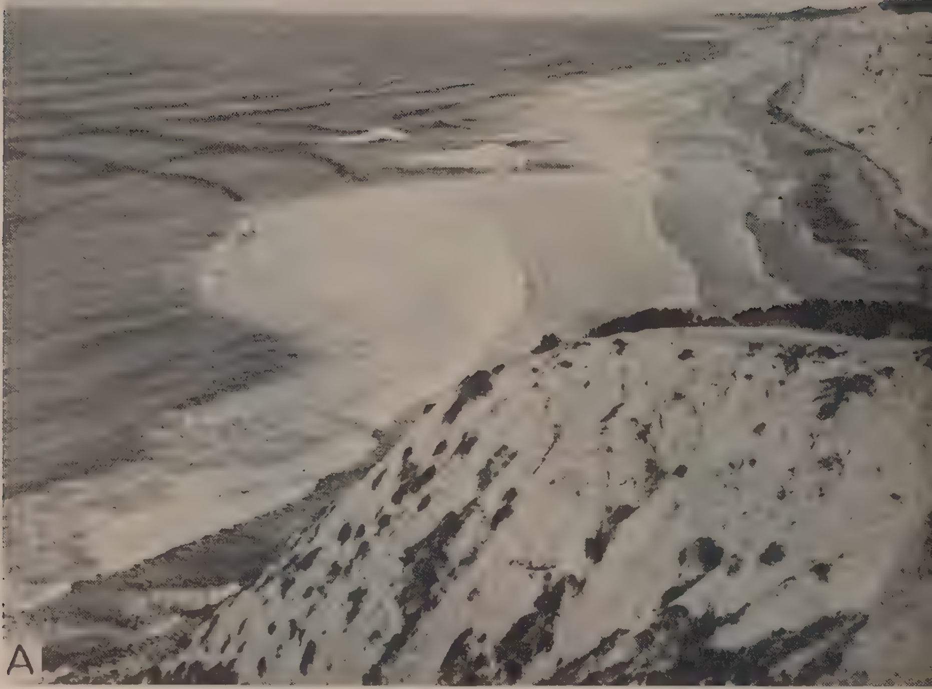
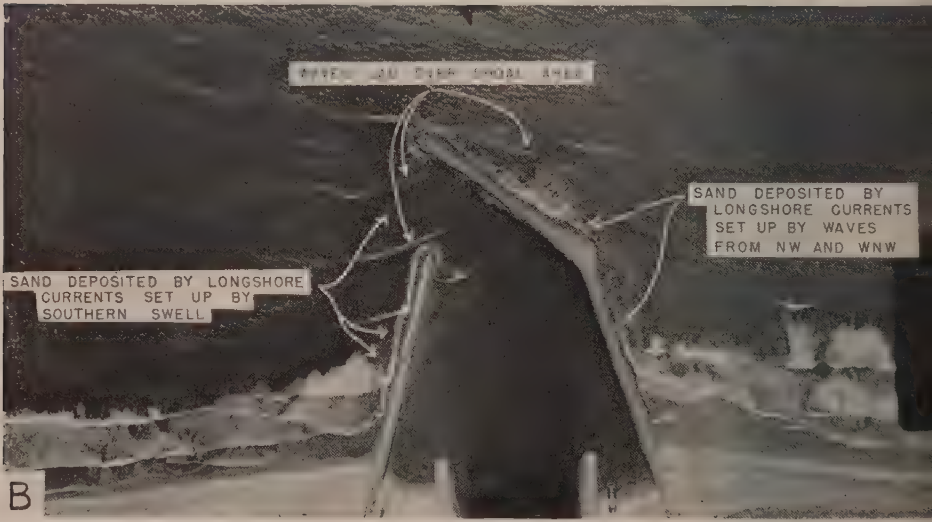

6 MAY 1944 -1005
1000 FEET
CREST LAG

PLATE VIII


A


[illegible] [illegible] OVER SHOAL AREA
SAND DEPOSITED BY LONGSHORE CURRENTS SET UP BY WAVES FROM NW AND WNW
SAND DEPOSITED BY LONGSHORE CURRENTS SET UP BY SOUTHERN SWELL
B

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NUTRITION, GROWTH AND SEXUALITY OF THE PISMO CLAM (TIVELA STULTORUM)

WESLEY R. COE

Osborn Zoological Laboratory, Yale University, and Scripps Institution of Oceanography, University of California[1]

FOUR FIGURES

The investigations of Yonge ('26, '35, '36) on the oyster and other pelecypods, Graham ('31) on the razor clam, Fox and Coe ('43) and Coe and Fox ('44) on the sea-mussel and Coe ('45a) on the bay-mussel have shown that in these ciliary-feeding bivalves most of the food is assimilated by the intracellular digestion of minute cells and organic particles. This is accomplished mainly by the large phagocytic cells of the digestive diverticula, supplemented to a small extent by migratory phagocytes in the lumen of the alimentary canal. Only starch and glycogen are digested in the stomach by the amylase and glycogenase, secreted by the cells of the style-sac and incorporated in the style. Extracellular cellulase is very weak or is not formed. Consequently dinoflagellates and other unicellular algae with cellulose walls, which are often ingested in vast numbers, are not assimilable in the living condition. Most of them are too large for intracellular digestion. However, their disintegration products after death add to the detritus which furnishes the principal part of the nutrition. Nor is there any satisfactory evidence of an extracellular protease which might digest organisms with naked protoplasm or other proteins in the lumen of the alimentary canal. The presence of the style indicates the absence of such an enzyme.

In order to determine to what extent these conditions apply to detritus-feeding bivalves with somewhat different habits, a study has been made of the Pismo clam. The rates of growth as correlated with the food supply, as well as with temperature and age, have also been investigated by examination of marked individuals living under natural conditions and by the collection of large samples of the population at intervals throughout the year. In order to disturb the population as little as possible, nearly all the clams were returned to the beach after the measurements had been made. Incidentally, the sexuality of the species, in regard to which some misconceptions have been published, was given particular attention. A detailed account of the economic aspects of the habits and growth of this species, which is one of the largest and most palatable of the bivalves on the coast of California, was published by Weymouth many years ago ('23). This was later supplemented by a report by Herrington ('30). The population at La Jolla, however, differs in many respects from that described in these reports.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, no. 308.

Pismo clams live only on the sandy beaches and sand bars of the open coast, which are fully exposed to the surf of the ocean. They are found near the middle of the intertidal zone and below to a depth of several meters at low tide, where they lie buried near the surface of the sand and feed on such minute organisms and organic particles as may be drawn by ciliary action into the inhalent siphon and thence to the mantle cavity. In passing over the gills the materials become imbedded in mucus, after which the sheets of mucus and their contained particles are either rejected by the labial palps or drawn into the mouth. The rejected materials are usually thrown out of the mantle cavity and from the shell along the posterior ventral edge of the mantle or expelled forcibly from the inhalent siphon. The feces are discharged in rodlike form from the exhalent siphon.

NUTRITION

The Pismo clam is a typical scavenger, or detritus feeder, although living unicellular organisms form no inconsiderable portion of the diet. Only minute cells and particles, both organic and inorganic, are ingested. The inhalent siphon is provided with an elaborate filtering mechanism, with sensitive branching papillae which prevent the entrance of larger particles into the mantle cavity. Such particles as are admitted undergo a further assortment by the palps which guard the entrance to the mouth.

The sorting depends largely on the size of the object, since particles of sand and small bits of shell seem to be as readily ingested as nutrient materials. In fact, more than half of the stomach and intestinal contents not infrequently consists of sand. Minute fragments of cellulose, portions of mollusk shells, sponge spicules, and spines of dinoflagellates and diatoms are often present. Particles of sand 0.2 to 0.3 mm in longest diameter, thin fragments of periostracum and chitin nearly 1 mm in length and filamentous algae 1½ mm long are the largest objects observed in the stomach.

In contrast with these relatively large objects, the mucous sheet secreted on the gills is so efficient that it can filter, from the water passing over the gills, particles of extreme minuteness, evidently including the smallest bacteria. MacGinitie ('45) has shown that the mucous net of the worm Urechis can filter out even the larger protein molecules. It is not improbable that in the pelecypods any particulate organic matter, not in true solution, can be collected by the mucous sheets and thereby ingested, although not all the particles entering the mantle cavity are caught by these sheets.

Particles of powdered carmine and other inert substances are readily taken into the mantle cavity but if they are in too dense suspensions most of them are rejected by the palps and discharged at the posterior ventral margin of the mantle. If the particles are less numerous they may be ingested and later discharged in the feces. Neither does feeding usually occur in dense suspensions of microorganisms, spermatozoa, ova, yolk or oil globules, or starch particles, although these are taken into the mantle cavity, imbedded in mucus in passing over the gills and then ejected without entering the mouth.

Of the living organisms ingested by the clam, the most abundant dinoflagellates are species of Prorocentrum, which are 0.04 to 0.05 mm in length, Gymnodinium, Peridinium, Gonyaulax, Dinophysis and many others which average 0.04 to 0.06 mm in diameter, while the species of Ceratium, which are spiny and 0.2 to 0.3 mm in length are excluded. Spherical algal cells as large as 0.1 to 0.3 mm in diameter are frequently found in stomach and intestine, as are also slender multicellular algae as long as 0.6 mm. Cryptomonads, phytomonads and other flagellates are generally much smaller. Solitary diatoms 0.05 to 0.2 mm in length and smaller are often ingested in large numbers but colonial and spiny species are commonly rejected. Other living cells include algal zoospores and the gametes of nearly all the invertebrates of the vicinity, including those of the clam itself.

In addition to the siphonal papillae and the labial palps, the ingested particles encounter a third sorting mechanism on reaching the stomach. This consists of a food-sorting caecum in which the particles are kept in rotation by ciliary action whereby the finest particles are carried toward the openings into the digestive diverticula, while the larger particles are diverted toward the intestine. The cilia also keep the end of the rotating style pressed against the gastric shield (Nelson, '18). This tends both to crush and comminute some of the softer particles and to squeeze any cytolysed particles out of the cell walls in which they may be contained. As the end of the style is worn away its enzymes are liberated.

By no means all of the ingested organic materials are capable of digestion, however, for the evidence indicates that the clam has but little capacity for digesting cellulose by extracellular secretions. Consequently such living dinoflagellates and other algae as are provided with cellulose cell walls may pass through the digestive canal and be extruded in the feces while still in the living condition. This is proved by the fact that flourishing cultures of the dinoflagellate Prorocentrum have been obtained when this organism was taken from the rectum, with precautions against contamination, and placed in sterile culture media. Ingestion does not imply digestion.

Examination of the stomach and intestinal contents after feeding with various materials leads to the conclusion that nutrition in the Pismo clam, as in the oyster (Yonge, '26), the mussels (Fox and Marks, '36; Fox and Coe, '43; Coe and Fox, '44; Coe, '45a) and most other pelecypods depends mainly on intracellular digestion. This is accomplished by the phagocytic cells of the digestive diverticula and to a much smaller extent by migratory phagocytes in the lumen of the digestive canal. As already mentioned, the enzymes in the stomach of most pelecypods are principally amylase and glycogenase secreted by the cells of the style sac and incorporated in the style. Chemical tests show that both these enzymes are present in the style and stomach juices of Tivela, together with a weak cellulase. Proof of the latter was obtained by freeing the cellulose of the alga Enteromorpha from other carbohydrates and digesting it with aqueous style extract for 24 hours or more at pH 6.3, equal to that of the clam's stomach. Toluene inhibited bacterial activity. Boiled extracts had no effect on the cellulose. The concentration of cellulase, however, is evidently too weak for effective action in the utilization of phytoplankton with cellulose walls. For assistance in making these tests the writer is indebted to Dr. Denis L. Fox and Mr. Sheldon C. Crane.

Although free lipase and protease were reported by Albrecht ('21) as occurring in the alimentary canal of this species, it now seems evident that these enzymes are utilized within the phagocytic cells and are not secreted into the lumen of the canal. It has been observed, however, that a number of phagocytes in the lumen of the stomach may gather about a diatom too large to be taken into any one of the cells. There is some evidence that they may then secrete their digestive enzymes upon their surfaces and thus render the object capable of direct assimilation by their cytoplasm. They may then return to the connective tissues of the body with their supplies of nutrition. The digestive diverticula in this species are not to be considered as organs for the secretion of free enzymes, although their phagocytic cells discharge into the digestive canal the indigestible remains of the phagocytized materials in addition to large numbers of minute brownish globules. The latter are presumably excretory in nature, for they are later discharged in the feces.

Intracellular digestion is the usual condition in pelecypods, although it should be mentioned that Mansour ('46) and Mansour-Bek ('46) have reported that the filtered, phagocyte-free stomach juices of Tridacna and Pinctada contain free proteolytic, lipolytic and carbohydrate-splitting enzymes. They also concluded that Ostrea, Mytilus and Unio are able to digest by extracellular secretions relatively large zooplankton such as copepods, which are sometimes found in a partly disintegrated condition in the stomach and intestine. Nevertheless Yonge ('46) maintains that the free enzymes which would be required for such digestion are not present in any of the species that he has examined. Greta and Sven Hörstadius ('40), however, have demonstrated that some species of gastropods obtain their nutriment by intracellular digestion, while others secrete their enzymes into the digestive canal.

While there is general agreement that the pelecypods, with the exception of the septibranchs, ingest both assimilable and unassimilable particles indiscriminately, there is much difference of opinion as to the relative contribution of the different constituents of the food supply to the animal's nutrition. The local supply of food materials utilizable by the Pismo clam has been determined during several years by frequent examinations of the stomach and intestinal contents and feces and by daily records of the phytoplankton populations present in the water and hence available for the clam. Dinoflagellates, diatoms, bacteria and other algae, minute zooplankton, gametes of invertebrates, zoospores of algae and detritus from the disintegration of plant and animal cells are commonly present in varying proportions.

Dinoflagellates. The average number of dinoflagellates in the water throughout the year in 1940 to 1943 was about 32,000 per liter. For periods of a few days the number reached 500,000 or more per liter. Even though the living cells cannot be utilized by the clam, their disintegration products after death doubtless contribute as detritus to the clam's nutrition. Some of the ingested cells are in process of cytolysis before ingestion and some of their disintegration products presumably become available while the cells are passing through the clam's digestive canal.

The computations of Fox and Coe ('43) indicate that approximately 60,000,000 dinoflagellates of average size would be required to furnish 1 gm of dry organic matter. This would imply that the clam would have to filter about 2,000 liters of water in order to obtain each gram of organic matter from the detritus of the dinoflagellates present. It is estimated that a 70-mm clam filters an average of 60 liters of water during its feeding times each day, or 2000 liters a month. It must not be assumed, however, that any large proportion of the detritus will be available in the locality where the living dinoflagellates are found, for the ocean currents are constantly transporting both the dinoflagellate populations and their decomposition products to and from the clam beds at an average rate of 4 to 5 miles a day.

Diatoms. In contrast with the dinoflagellates, the diatoms are without cellulose walls and many of them are so small as to be capable of intracellular digestion. The water contains a yearly average of about 30,000 diatoms per liter but many of them are too large or too spiny to be ingested. Nevertheless their average size is so small that it is estimated that 600,000,000 could furnish only about 1 gm of dry organic matter. At the rate of filtration of 60 liters of water per day, a 70-mm clam could obtain from this source only a little more than 1 gm of organic matter in a year, even if all the diatoms could be ingested and assimilated. Hence the available supply can contribute only a small part of the clam's nutritive requirements, either as living cells or as detritus.

Bacteria. Although the water contains an average of about 45,000,000 bacterial cells per liter and these are directly utilizable, their size is so minute that they furnish only a small amount of organic matter. It is quite possible however that they may supply nutritive elements not otherwise available.

Zooplankton. Many species of minute flagellates are often abundant and suitable for intracellular digestion. Larger zooplankton, including larvae of invertebrates, is utilizable only after disintegration.

Gametes of invertebrates and zoospores of algae. These are from time to time available in greater numbers than the clam is capable of assimilating and at such times furnish an abundant supply of nutriment, both as living cells and as detritus.

Detritus. Unidentifiable particles of organic matter, evidently derived from the disintegration of plant and animal cells are always present in stomach and intestine. Every plant and animal living in the sea contributes to this detritus, during life by its reproductive cells and waste products and after death by its dissociated cells. There can be no doubt that these lifeless organic particles furnish a large proportion of the nutriment of all the filter-feeding pelecypods. The detritus may be either of local origin or brought from a distance by the ocean currents.

Analysis of the water in the vicinity of the clam beds shows that it contains an average of about 5 mg of total organic matter per liter. Some of it is in solution and becomes available only through the agency of microorganisms. The amount, however, is subject to rapid fluctuation and it may increase several fold within a few hours by the simultaneous liberation of gametes by vast numbers of algae or invertebrates, as well as by the death and disintegration of animals or plants in the vicinity. It may also be increased or decreased to an equal extent as the currents bring or carry away exceptionally large amounts of organic materials. Assuming again that, while feeding, a clam 70 mm in length filters 60 liters of water daily, it might be possible for it to obtain about 0.3 gm of potential nutriment a day, provided all the organic material in the water were capable of ingestion and assimilation. But, as has already been indicated, only a small fraction of it can be utilized directly by the clam.

Nevertheless the daily requirements of the clam are very small, except when the gametes are being formed. The dry organic matter in a 70-mm clam weighs only 1.5 to 2.9 gm and this has required 3 years or more for its up-building. In the meantime, of course, the normal metabolism of the clam has expended most of the nutriment assimilated. At the end of its first year of life, when the shell is about 21 mm in length, the dry weight of its organic matter averages only 0.06 to 0.08 gm. At 2 years of age and 42 mm in length the dry weight of the tissues has increased to 0.5 to 0.7 gm.

As the gonads commence the formation of gametes in the spring the weight increases and continues to do so until spawning begins late in the summer. The dry weight of organic matter in the ripe gonads is nearly half that of all the other tissues of the body, exclusive of the shell.

In addition to the food energy required for the formation of the tissues and reproductive cells, a considerable amount must be expended in the secretion of the shell. Correlated with the rugged environment which the clam must endure is a relatively much thicker shell than in most other pelecypods. The weight of the shell at all ages is 20 to 30 times as great as that of the dry tissues of the body.

GROWTH

A. Rates of growth as determined by marked individuals

It is obvious that direct observations on the rate of increase of marked individuals living under natural conditions will furnish the most reliable measurement of the growth rate.

Some difficulties are involved in such observations on this species because the rapid shifting of the sand on the beach often makes the recovery of marked individuals uncertain. This was largely overcome by planting many of the marked clams in an enclosure of heavy wire mesh. In the absence of heavy surf, however, the marked clams remained in or near the place where planted for several months without restraining wire.

A total of 558 individuals with shells marked to indicate size and date were planted at monthly intervals. Many of these were lost but the others were examined each month and the increment in length recorded. The rates observed in the 30 or more individuals recovered each month conformed rather closely with the averages of random samples of the same ages in the population at the same season, as reported in the following section.

These marked individuals clearly demonstrated that relatively little growth occurs during the winter. The average increment in length was less than 1 mm a month. In April and May, as the seas became calmer and the water warmer, the monthly rate was more than 2 mm, while in June it reached an average of 2.6 mm, the highest of the year. Each of several individuals increased their lengths by 4 mm or more in a month. The rate diminished during July and August, the early part of the spawning season, but increased again in September (figs. 1, 2).

As was reported from similar studies on the growth rates of mussels (Coe and Fox, '44; Coe, '45a) some individuals grew rapidly for a time and were then overtaken by others. Some continued comparatively rapid growth, while others of the same ages remained dwarfed. The total increment in length for clams in their second and third years, as determined by marked individuals and population samples, showed an average of only 8.7 mm during the 6 months preceding the end of March and 12.4 during the following half year, making a total of 21.1 mm for the entire year. The increments for each month, beginning with September, were 2.3, 2.0, 1.6, 1.2, 0.9, 0.7, 1.4, 2.2, 2.4, 2.6, 2.0, and 1.8 mm, respectively (table 1, fig. 1).

Seasonal variation and temperature. Although, as indicated in figure 1, there is a difference of only about 8°C. in the average temperature of the water in the coolest and warmest months of the year, the growth rates corresponded rather closely with the season for 2 reasons. First, because the coolest months in winter are coincident with the season of storms, heavy surf and shifting sand, which interfere with continuous feeding. Second, because the available food supply is reduced at that season (Coe and Fox, '44).

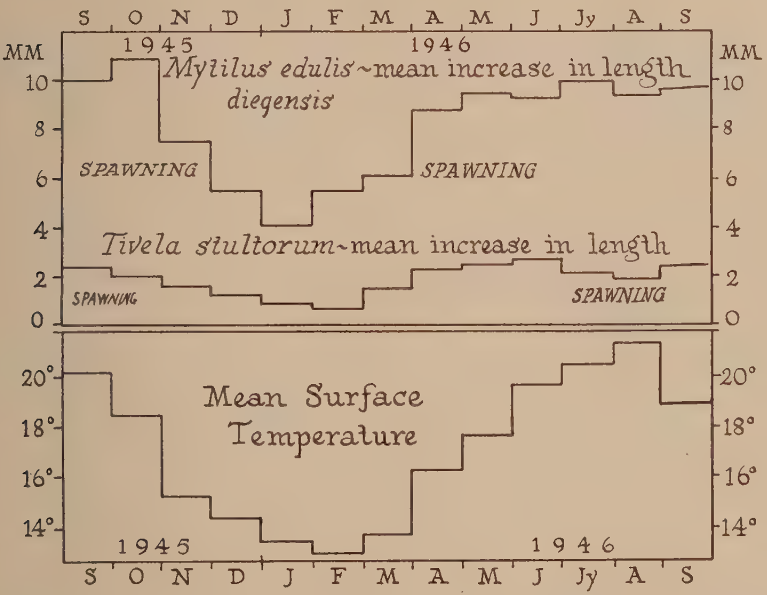

Fig. 1 Correlation between growth rates of the Pismo clam and the bay-mussel with the mean water temperature for each month of the year beginning in September. As compared with that of the mussel the growth of the clam is very slow. In both species the rate decreased in August, the month with highest temperature.

With increasing temperature and increasing solar radiation in the spring the seas become calmer, the phytoplankton and

TABLE 1

Proportions of Pismo clams of different age groups in the population on the Scripps Institution beach, omitting those more than 4 years old.

DATE [1]	AGE MONTHS	NO. INDIV.	MEAN LENGHT AND VARIATION	AGE MONTHS	NO. INDIV.	MEAN LENGHT AND VARIATION	AGE MONTHS	NO. INDIV.	MEAN LENGHT AND VARIATION	AGE MONTHS	NO. INDIV.	MEAN LENGHT AND VARIATION
			mm			*mm*			*mm*			*mm*
1945												
Sept. 30	12	195	20.9 (11–29)	24	38	42.0 (30–51)	36	21	58.5 (53–65)	48	3	77.3 (77–78)
Dec. 31	3	336 [2]	5.2 (4–7)	15	82	26.4 (16–38)	27	20	46.9 (42–51)	39	4	63.5 (60–65)
1946												
Mar. 31	6	361	8.3 (4–13)	18	97	29.5 (17–41)	30	25	48.9 (42–60)	42	9	65.7 (61–70)
May 31	8	221	12.1 (5–20)	20	88	33.4 (21–45)	32	19	53.4 (46–61)	44	6	66.2 (64–70)
June 30	9	120	14.8 (6–20)	21	34	36.1 (22–45)	33	10	56.8 (46–63)	45	5	67.4 (65–69)
July 15	9½	243	16.3 (7–22)	21½	78	37.3 (22–51)	33½	14	57.1 (52–60)	45½	2	71.0 (70–72)
July 31	10	162	17.3 (7–23)	22	33	37.7 (24–49)	34	17	58.1 (51–65)	46	0	. . .
Aug. 15	10½	306	17.8 (9–27)	22½	61	38.5 (27–46)	34½	14	58.6 (49–60)	46½	2	73.0 (70–76)
Aug. 31	11	199	18.5 (12–27)	23	38	39.9 (28–50)	35	9	59.5 (50–64)	47	4	75.7 (64–79)
Sept. 30	12	247	21.2 (14–28)	24	61	42.3 (29–50)	36	12	61.8 (52–68)	48	3	78.4 (71–88)
Oct. 31	13	151	23.2 (16–33)	25	36	43.9 (31–53)	37	4	62.0 (57–64)	49	0	. . . .
Total no. indiv.		2541			646			165			38	

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[1] The date indicated is the average of the 2 or more days on which the collections were made, according to the tide.

zooplankton are more abundant and the reproductive elements of algae and invertebrates become available in increasing quantity. This, as mentioned, is the season of most rapid growth (figs. 1, 2).

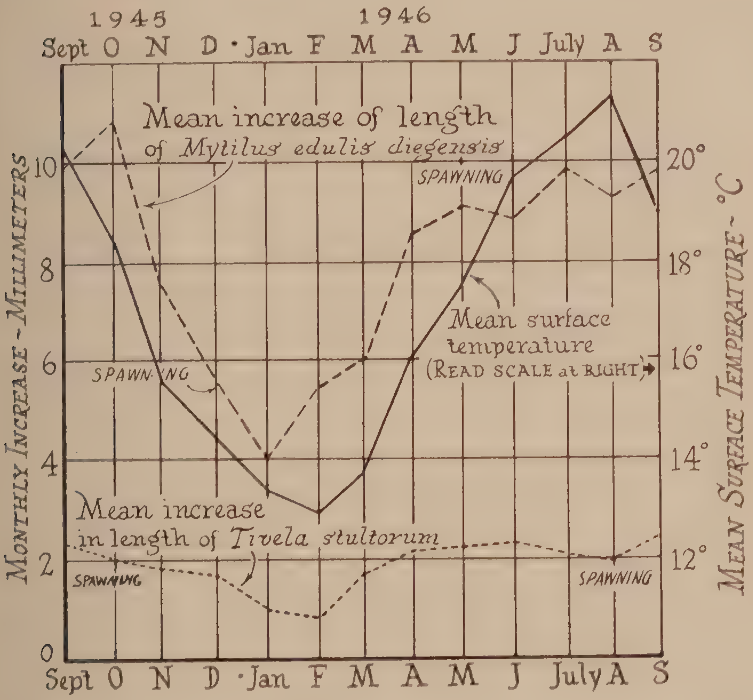

Fig. 2 Comparison of growth rates of the Pismo clam and the bay-mussel in relation to the temperature of the water.

Although the temperature rises to a maximum in August, accompanied by almost invariably calm seas and abundant nutrition, the growth rate diminished appreciably. This decrease appears to be due to the requirements of the reproductive system and the successive acts of spawning. The decreased rate is frequently marked on the shell by a "growth" ring.

In September the growth rate rose sharply, to decrease in successive months as the temperature fell to a minimum in February (fig. 2). The phytoplankton showed a similar decrease. This bimodal periodicity in growth rate is parallel with that of the sea-mussel and of many of the associated invertebrates (Coe and Fox, '44).

B. Rates of growth as estimated by large samples of the population

In order to avoid the influence of different beach levels and other local conditions on the growth rate, the collections were all made in the same area and near the low-tide level. To maintain the population as nearly undisturbed as possible, nearly all the clams were returned to the same part of the beach after the measurements had been made. Since this is a restricted natural preserve, there was presumably no molestation by human agencies. The significant data from 11 of these collections, with a total of 3390 individuals, are given in table 1.

For the reasons stated in the section on reproduction, the ages of the young clams are calculated from the end of September, this being the average date when the newly metamorphosed individuals begin their growth after settling in the sand. During the first half year the shells remain so small that they are difficult to find in the shifting sand. Samples collected in December had an average length of 5.2 mm. Three months later, when their average age was 6 months, the shells varied from 4 to 13 mm in length, with a mean length of 8.3 mm (table 1, fig. 3). This would indicate an average initial growth rate of 1.38 mm a month.

When 1 year old the length varied from 11 to 29 mm, with an average of about 21 mm. At the age of 1½ years the mean length is approximately 30 mm, and at 2 years 42 mm, with a maximum of 51 mm. The mean length when 3 years old is about 61 mm, with a maximum of 68 mm or more, and at the age of 4 years 71–88 mm (table 1, figs. 3, 4).

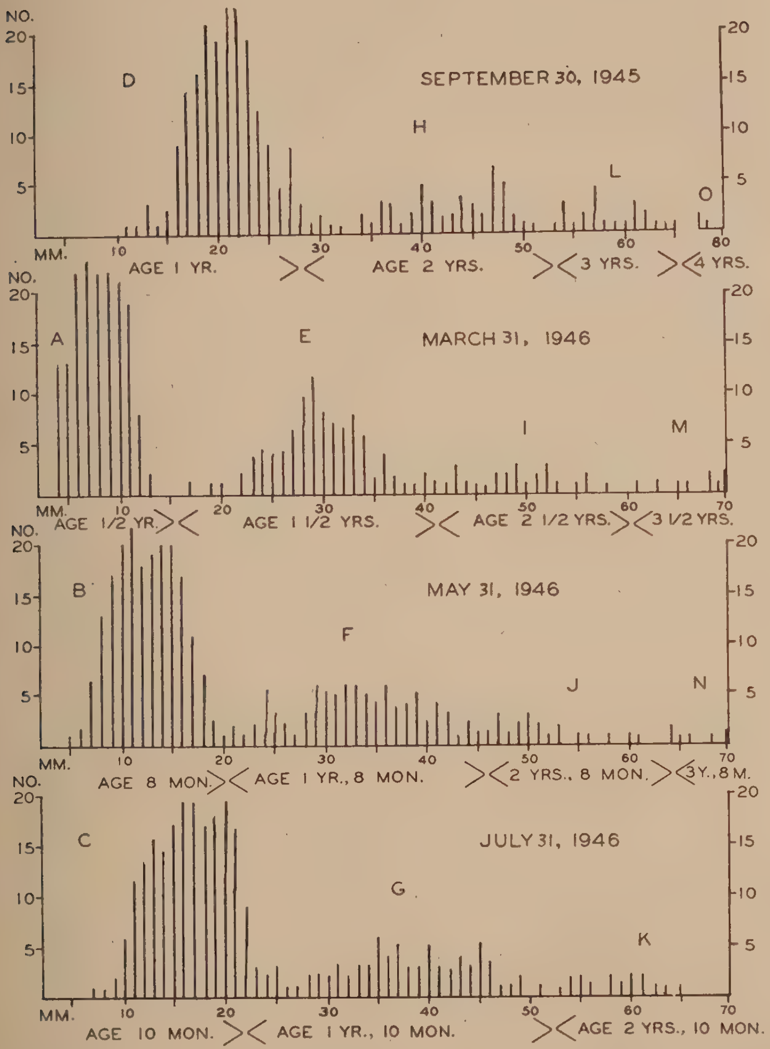

Fig. 3 Variations in the ages and sizes of the population of Pismo clams on the Scripps Institution beach (La Jolla, California) in samples collected in September, 1945, and in March, May and July, 1946. Individuals more than 4 years of age are omitted. The rates of growth of each age group and the decreased proportions with advancing age are clearly indicated.

The relatively few individuals 5 and 6 years old which were found on this beach averaged 95 and 112 mm in length, respectively. Some individuals reach the legal length of 5 inches when 5 years of age, but more frequently when 6 or 7 years old. Older individuals are even less abundant. The largest found were 140 to 148 mm in length, with an estimated age of at least 12 years. Because of variations in the environmental conditions the growth rates may vary considerably from year to year for clams of the same ages (table 1).

Weymouth ('23) concluded from an examination of the growth rings that the average length at Pismo and Oceano during the first winter, when 4 to 6 months of age, was 22 mm and during the second winter was 45 mm, but he was doubtless in error as to the ages. The average increment in the third year was estimated as 20.2 mm and in the fourth year 17.8 mm, the minimum legal length being attained in 4 to 7 years He observed a maximum length of 175 mm and estimated that some of the largest individuals were 18 to 25 years old.

As compared with some of the other pelecypods in this locality the clams have a relatively low rate of growth. Under favorable conditions the sea-mussel (Mytilus californianus) may become 60 to 86 mm in length at the age of 1 year (Coe and Fox, '42) and the bay-mussel (M. edulis diegensis) 66 to 76 mm (Coe, '45a) or occasionally 82 mm (Coe, '46) at the same age (fig. 2). In less favorable situations the growth rate is less than one-fourth as great and in every large group there may be some individuals that remain dwarfs even under optimum conditions. Some are as large when 2 months old as others at the age of a year. The normal growth curve of the clam as compared with that of the sea-mussel and of the bay-mussel is shown in figure 4.

Such variability has been reported for many other mollusks. The soft-shell clam (Mya arenaria) on the southern coast of New England may reach a length of 40 to 48 mm at the age of 4 months and a length of 60 to 80 mm when 1 year old, while other individuals, less favorably situated, may be only 8 to 20 mm long when spawning at the end of their first year (Coe and Turner, '38).

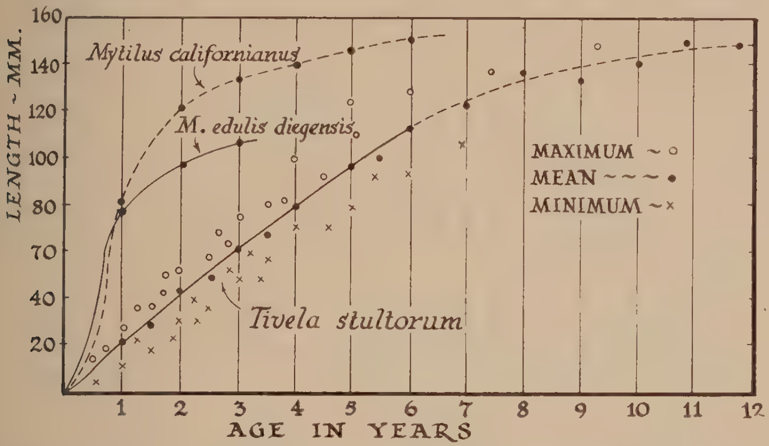

Fig. 4 Growth curve of the Pismo clam, based on measurements of more than 3000 individuals. Corresponding curves of the growth of the sea-mussel and the bay-mussel from the pier adjacent to the clam beds are indicated for comparison.

THE POPULATION

Fluctuations in abundance

Weymouth ('23), Herrington ('30), Clark ('32), Roedel ('39) and others have emphasized the wide fluctuations in the numbers and age groups constituting the populations from year to year. Similar fluctuations occur at La Jolla, not only in the Pismo clam but in most of the other pelecypods of the locality (Coe, '46). Periods of abundance are followed by periods of scarcity due, presumably, to variations in environmental conditions, particularly during the free-swimming larval period. The set in 1 year may be several times as great as in the following year.

The relative proportions of clams of different ages found on a limited portion of the beach at intervals during the year 1945–6 are shown in table 1 and figure 3. As previously mentioned, these collections consisting of a total of 3390 individuals did not deplete the population, since nearly all were returned to the same area on the beach after the measurements had been taken.

Table 1 shows that in most of the 11 collections there were approximately 4 times as many individuals in each age group as in the group 1 year older. The percentage in their first, second, third and fourth years was about 76, 19, 5 and 1, respectively. It might be concluded therefore that about three-fourths of the members of each age group disappear from the intertidal zone each year. Such a conclusion is not entirely justified however because the set in 1944 was larger than in the preceding years and that in 1945 was even larger than in 1944.

Nevertheless it is obvious that a differential mortality rate may change the ratios rapidly. Such an event was observed about the middle of August, 1946, when Prorocentrum and other dinoflagellates appeared in sufficient numbers as to discolor the water. Two days later it was estimated that the empty shells of more than 50,000 yearling clams had been washed up on a beach about a mile in length. Assuming that there had been a half million yearlings in that area previously, it is probable that this age group had been decimated, with only a small loss of clams of older ages. But this is not considered as satisfactory evidence that the dinoflagellates alone were responsible.

The rate of disappearance even from this legally protected beach during the first 5 years of life has generally been almost equal to the productivity of the population. Some individuals are washed by the surf into deeper water where they are not readily obtainable; others are left stranded high up on the beach. Many are destroyed by gulls, crabs, various elasmobranchs and other fishes, which constitute their principal natural enemies. The only evidence of parasitic diseases that has been found was the presence of occasional trematodes.

Legally protected areas have little direct influence on the setting of young clams within those areas, since the prevailing ocean currents may carry the free-swimming larvae a distance of 50 miles or more from their place of origin before the young clams are ready to settle in the sand. The beneficial effects of such restricted areas are correspondingly widely distributed.

Growth rings; disturbance rings

The shells of many individuals are marked by concentric rings of alternating darker and lighter coloration, usually associated with corresponding surface corrugations. At irregular intervals the general opacity of the shell is interrupted by translucent rings, best seen by transmitted light. These translucent rings indicate periods of major disturbance and retarded growth and are sometimes accompanied by injuries which occurred on the edge of the shell.

By the examination of marked shells at successive periods of growth it has been found that both minor and major rings may be formed at any season of the year, sometimes as the result of changes in the level of the sand or being washed out of the sand by heavy surf, with consequent interruption of feeding and withdrawal of the mantle from the edge of the shell. When growth is resumed the new shell is not directly continuous with that previously deposited but underlies the latter and projects beyond it, forming a slightly raised ring. The color may differ conspicuously from that of the adjacent portion of the shell. A more or less conspicuous ring is formed each time the clam is brought into the laboratory for measurement.

Similar rings are formed in the summer when the sea remains calm and there is little physical disturbance of the sand. These are evidently due to physiological processes associated with the reproductive period. These summer rings are often more conspicuous than those which result from physical disturbances. In species of Pecten and in some other bivalves the principal annual ring is formed during the reproductive season. As a general rule 1 distinct summer ring and 1 or more winter rings are formed each year in this locality. If the date of collection, together with the average growth rate at that age and that season are known, the date when the last ring was formed can be determined by measuring the space between the ring and the ventral margin, since the new growth retains the normal symmetry of the shell, in which the ratio of height to length remains approximately 3:4 at all ages. The many minor rings, often with accompanying change of color, are presumably due to a physiological rhythm of periods of shell secretion and pigment formation.

SEXUALITY

Weymouth ('23) concluded that the Pismo clam is normally hermaphroditic, although he admitted that he had made no careful histological examination of the gonads. He stated further that the coexistence of mature eggs and active sperm, though observed, was not general, there being usually only a few mature eggs when active sperm were abundant. He suspected that eggs and sperm were produced in succession by each individual during the season.

These conclusions are not supported by more recent investigations, for it is now evident that ambisexuality seldom occurs in this species, either on the beach at La Jolla or at Oceano and Pismo where Weymouth's material was obtained. On the coast of Mexico the species is likewise unisexual. A thorough examination of the gonads of 332 individuals during all parts of the year and at all ages up to 10 years or more has revealed only 3 hermaphrodites, the remaining 329 being strictly unisexual. The 3 ambisexual individuals were in their first spawning season, one of them being 19 mm, another 22 mm and the third 25 mm in length. In 2 of these the gonads were predominanty female, with only a few spermatic follicles. The third was male with the exception of 3 ovarian follicles. No mixed follicles were present in any of the 3.

There can be no reasonable doubt that these three ambisexual individuals are examples of accidental failure of the sex-differentiating mechanism during development. Such developmental ambisexuality has been reported in nearly all groups of plants and animals, including most of the species of pelecypods in which large numbers of individuals have been examined (Coe, '43, '45). It is more frequent in young than in older individuals.

In several species of pelecypods local races have been reported which differ genetically in the expression of sexuality, one of the races being ambisexual and the other unisexual. Because of Weymouth's conclusion it was formerly thought that the Pismo clam at Oceano-Pismo might be of a different sexual race than the population at La Jolla but, as already stated, no evidence of such differences has been found. As has been commonly reported for other pelecypods, as well as for many groups of animals, adult female clams appear to be somewhat more numerous than males. Among the 329 unisexual individuals mentioned, there were 180 females and 149 males. In the yearling population no significant size differences could be detected between the males and the females, although in the Virginia oyster the young females usually grow faster than the males (Coe, '43, '45) and in the sea-mussel the males average somewhat larger than females of the same age (Coe and Fox, '42).

The reproductive season in this locality extends from about the middle of July to the end of November, although there seems to be but little spawning before the first of August, and most individuals have retained only a few residual gametes after the middle of November. The most abundant spawning usually takes place in September. Assuming a free-swimming larval period of about 3 weeks, it may be concluded that the average date of settlement of the metamorphosed young clams in the sand is near the end of September, and that date has been used in reckoning the age.

Nearly all individuals become sexually mature and spawn when 1 year of age, many of them when only 17 to 20 mm in length. Both Weymouth ('23) and Herrington ('30) erroneously concluded that the first spawning occurs at the age of 2 or 3 years. A few of the smallest and most retarded individuals have only immature gametes in November, when spawning has been completed in the other members of the population, and it is doubtful whether any of their gametes are discharged. As is usual in pelecypods, each individual experiences several spawning periods during the season, since only a portion of the gametes are mature at the first period of ovulation or sperm emission. Older individuals usually spawn earlier and have a longer spawning season than yearlings. Some residual gametes always remain after the final spawning and these are absorbed during the winter.

Laboratory experiments prove that the emission of gametes by 1 individual, particularly by a male, stimulates the concurrent spawning of other individuals of both sexes in the vicinity. This is obviously conducive to the successful fertilization of the millions of ova which each large female liberates in a single spawning period.

In young individuals, gametogenesis is inaugurated in March or April at the age of about 6 months, and when the shell is only 7 to 13 mm in length. In older individuals the gonads remain inactive and inconspicuous during the winter, rapid proliferation and differentiation of the gametogenic cells beginning early in March. The males usually have a few motile spermatozoa and the females some nearly mature ova in April or May. During the next 2 months the gonads increase rapidly in size and the proportion of mature gametes becomes larger as the first spawning period in July or August approaches. The fully mature ova measure 0.07 to 0.078 mm in diameter. Attempts to induce spawning have sometimes been successful with both sexes, either by gametic stimulation or otherwise, although an occasional individual of either sex may spawn spontaneously when returned to water after having been kept for a few hours in the air. Normal development has not been obtained from eggs cut from the ovary and fertilized. Eggs which have passed through the oviduct however develop into normal embryos under experimental conditions.

SUMMARY

The Pismo clam is a typical scavenger, ingesting only minute organisms and cells, together with both organic and inorganic particles. Digestion is mainly intracellular and is accomplished principally by the phagocytic cells of the digestive diverticula, aided by migratory phagocytes in the lumen of the alimentary canal.

The principal extracellular enzymes in the canal are amylase and glycogenase incorporated in the style. The style also supplies a weak cellulase which is slowly effective on algal cellulose but is evidently inadequate for the digestion of dinoflagellates and other phytoplankton with cellulose walls, for most of these cells pass through the body without apparent change, some of them in viable condition. Diatoms, bacteria, flagellates and other minute protozoa, gametes of algae and invertebrates, as well as detritus from the disintegration of the cells of all marine plants and animals are the principal sources of nutrition. The detritus may originate locally or it may be brought from a distance by ocean currents.

Marked individuals living under natural conditions, as well as the entire population, increased their average lengths approximately 21 mm a year for their first 3 years of life and at a somewhat lower rate thereafter. The rates show a general correlation with the temperature and with the food supply.

The species is unisexual, with less than 1% developmental ambisexuality.

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INCREASE IN THE PERIOD OF WAVES TRAVELING OVER LARGE DISTANCES: WITH APPLICATIONS TO TSUNAMIS, SWELL, AND SEISMIC SURFACE WAVES

Walter H. Munk

(Contribution from the Scripps Institution of Oceanography, New Series, No. 309. This work represents results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the United States Navy Department under contract with the University of California.)

Abstract--An expression is derived from very general assumptions for the increase n wave period during long-distance propagation. To illustrate the general nature of the olution, application is made to three different geophysical phenomena: First, to the sunami from the Aleutian earthquake of April 1, 1946; second, to the long forerunners f the swell recorded at the wave station in Pendeen, England; and finally to the seismic urface waves from the Montana earthquake of June 28, 1925, and a smaller Mexican hock in 1943. In the case of the tsunami and the swell, observations and theory are in ood agreement. For the seismic surface waves the theory gives at least the right rder of magnitude. Application of the theory to the period increase of swell seems urthermore to provide a simple, rational basis for locating and tracking storms at sea y means of swell observations, and may therefore be of interest in weather forecasting.

ntroduction--Changes in wave period have been noticed for many types of wave propagation. ENBERG [see "References" at end of paper, 1929] has summarized some of the observations ives as examples the propagation of swell, microseisms, ordinary seismic waves, and sound s from explosions. Changes in wave period appear to be truly geophysical phenomena, notice- nly when dealing with waves traveling for long times over long distances.

he present paper attempts to explain these changes as the consequence of wave dispersion, s, as the result of the dependence of wave velocity upon wave period. The only assumptions ust be made are that (1) individual waves maintain their identity, and (2) at some given time ave period changes with distance. Under these conditions it is shown that dispersion must o an increase in period of an individual wave. Although the concepts of "dispersion" and od increase" have been previously connected by several authors, they seem not to have noted ffect upon individual waves, and for that reason have sought explanation in internal friction r than dispersion [RICHTER, 1943].

he effect of dispersion on wave period is first considered from a qualitative point of view. ate of period increase is then derived quantitatively in very general terms from the assump- hat the wave crests maintain their identity. The solutions are applied to three specific prob- for which they can be checked by observations.

The first application deals with tsunamis, a type of wave motion not ordinarily considered dis- ve. However, a slight dependence of the velocity upon period suffices to bring about measur- changes in period over long distances, and the observed changes can be brought into accord theory. A method is suggested whereby the nature and size of the original disturbance may timated from the tidal record at any given station.

The second application deals with long, low waves which appear to precede the visible swell a storm. These forerunners of the swell, which have been recorded at newly established stations at Pendeen, England, and Woods Hole, Massachusetts, obey the general dispersion The theory can also be applied to trace storms across the ocean by means of these wave rds. The computed path of two actual storms is shown to be in good agreement with the ob- ations on weather maps. The application towards a practical system of storm warning is ly discussed.

The third application deals with seismic surface waves. Good records from a large number ismograph stations make it possible to measure the period changes with somewhat greater sion than for tsunamis and swell, but this advantage is more than offset by the lack of a dependable analytic expression for dispersion. The relationship between velocity and period to be found from observations, and these give only a very approximate answer. Within the limi tions thus imposed, theory and observations of the period increase of seismic surface waves a consistent.

The principles can also be applied to other types of wave motion, indeed to any wave mot for which individual waves maintain their identity and for which the velocity depends to any deg no matter how slight, upon wave period. Observed changes in period may offer a powerful t for computing the dependence of wave velocity upon period and thereby describing some of th characteristics of the transmitting medium. The wide applicability derives from the general n of the basic equation, to which Rossby has applied the descriptive term "wave equation of co tinuity."

Only the kinematics of wave motion will be considered, that is, no attention will be paid t problems involving wave height. The relationships between group velocity, phase velocity, an energy propagation have been investigated in a fundamental paper by ROSSBY [1945] to which w shall make frequent reference.

Nature of the period increase--A number of attempts have been made to explain the increa in wave period in terms of a shift in spectrum brought about by viscosity. This point of v has been summarized by RICHTER [1943] (underscore mine): "Some extension of theory i required to account for the frequent observation that the prevailing periods of all types of seisn waves increase with distance. This cannot wholly be due to the normal spreading of an impulsi disturbance with filtering out of the shorter periods. . . . Surface waves show dispersion, the theory showing that velocity should vary with period; but this cannot account for the increase w distance of the period of a clearly identifiable wave group. . . . The required effect will be giv by some type of viscosity, or internal friction."

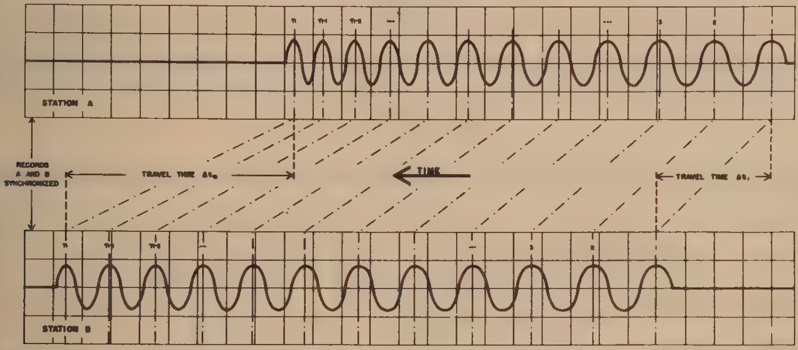
The reason why this approach has not led to tangible results lies perhaps in a misundersta ing regarding the true significance of the period spectrum for an impulsively generated distur ance. The shift of this spectrum has, in general, nothing to do with viscosity, and, furthermo does not relate to the changes of the recorded wave period except through a series of very com mathematical manipulations. The misunderstanding can be avoided by referring directly to t classical investigations by Cauchy and Poisson [LAMB, 1932, pp. 384-394] on waves produced local surface disturbance in deep water.

For an initial displacement of the free surface, which at the time $t = 0$ is assumed to be co fined to the immediate neighborhood of the origin $x = 0$, the disturbance of the sea surface at a time t and distance x is given by the Fourier integral $\eta(x, t) = (8\pi/g) \int_{\infty}^{0}(1/T_c^3) \cos (4\pi^2 x/gT$ $\cos (2\pi t/T_c) dT_c$. The symbol T_c denotes the period of the underlying spectrum. By means of several ingenious approximations the foregoing integral has been evaluated; $\eta(x, t) = (t/2) \sqrt{g/}$ $\cos (gt^2/4x - \pi/4)$, provided gt^2 is large compared to x. In regions where this formula holds, changes in height and period from wave to wave are very gradual. For a fixed value of x a wa crest passes at a time t_1, if $gt_1{}^2/4x - \pi/4 = 2\pi n$, and the following crest at a time t_2, if $gt_2{}^2/4$ $\pi/4 = 2\pi(n + 1)$, where n is any integer. Let T_r, the recorded wave period, be defined as the t interval between successive maxima (or minima) at a fixed point. It follows that $T_r \equiv t_2 - t_1 =$ $4\pi x/g\bar{t}$, where $\bar{t}$ is the mean of t_1 and t_2.

This very brief review of the classical method should serve to point out the difference bet the period T_c of the underlying spectrum, and the period T_r of the recorded waves. Accordin we shall speak of component periods and recorded periods. It is important to note that the und lying wave system is not in any simple manner discernible in the recorded waves, and may ind be regarded as a mathematical abstraction.

It is not proper to speak of an increase in the component periods, since all periods betwe zero and infinity are assumed to be present at all times in the Fourier integral expression. Ho ever, different component periods are associated with variable amounts of energy. At first m of the energy is concentrated in the shorter component periods, but a gradual shift takes plac toward the longer component periods. This shift follows directly from the dynamics of the pro lem, and does not involve, as is frequently supposed, the higher attenuation of short compone periods. Furthermore, a knowledge of this energy shift, and of the selective attenuation if th er is important enough to be included, does not offer any direct evidence concerning an increase he recorded periods. But by dealing directly with the recorded wave periods an increase in iod can be explained by the following elementary reasoning.

A group of n waves arrives at station A. The first crest passes at a time $t = 0$, succeeding sts at diminishing intervals $T_1, T_2, \ldots T_n$. This is typical of wave systems generated im- sively. Assume that the recorded period T_r at A decreases linearly with time according to the ation $T_r = T_1 - mt$. The upper portion of Figure 1 shows such a wave system for a constant plitude. The record is assumed to move from left to right, so that t increases from right to



1--Schematic presentation of an increase in wave period between stations A and B, showing xcess in velocity of longer waves over velocity of shorter waves, causing stretching of entire ave group

Assume, furthermore, that the propagation is dispersive; for this simple illustration let the e velocity C be proportional to the recorded period; $C = pT_r$.

The first wave has the longest recorded period and the greatest velocity. It will travel over a ll distance X between stations A and B in a short time interval, $\Delta t_1 = X/C_1 = X/pT_1$. The last e, which arrives at A at the time t_n, travels much slower and will take a time interval $= X/C_n = X/p(T_1 - mt_n)$ to travel from A to B. In Figure 1, $T_n = T_1/2$, and therefore $\Delta t_n =$ 1. The duration of the record at B will exceed the duration at A by $\Delta t_n - \Delta t_1$. Since the number aves in the record is the same, the average increase in the recorded period equals (Δt_n -)/n.

The foregoing discussion would have been more accurate if C_i in the expression for Δt_i had been computed from the period T_i at station A, but the mean period of the i^{th} wave between ions A and B. But even without the precise differential formulation which follows in the next tion, the above considerations show that the wave group "stretches." The result is not merely ift in spectrum from short to long periods; it is an actual increase of the average recorded iod of the waves in the group, and of all individual waves comprising the group.

The formulation of the problem depends therefore upon whether one deals directly with the sical deformations of the transmitting medium, such as we have done, or whether one considers ectrum of underlying constant-period wave systems, as in the Cauchy and Poisson analyses. e first case one deals with the recorded period, representing the time interval between two cessive maxima (or minima) at a fixed point; in the second case one deals with component iods which are found by generalizing a given portion of a record into a Fourier integral. In the t case wave periods increase, in the second case they remain constant.

For a complete solution, involving wave height as well as wave period, one must follow the hod of Cauchy and Poisson. The problem in its simplest two-dimensional form is not an easy and attempts to extend the investigation to the case of a finite initial disturbance [BURNSIDE, 3] or finite depth [PIDDUCK, 1912] have met with great difficulties. By dealing directly with recorded deformations, without recourse to any underlying spectrum, certain problems can be ted which are too complicated for a complete analysis of the Cauchy-Poisson type. ("In any r problem of wave motion in a dispersive medium we can do little more than argue by analogy e special problem of waves in deep water . . . " [LOVE, 1911].) The method permits the com- tion of the period increase for individual waves. Good agreement between the computed and erved values offers strong evidence that the phenomenon is inherent in the kinematics of wave ion, and is not related to the viscous properties of the transmitting medium. The following tion is devoted to a mathematical formulation of these principles.

Derivation of the basic equations

Changes in wave length--The wave length, L, of a wave traveling with phase velocity C along the positive x axis changes at the rate

$$\frac{dL}{dt} = \frac{\partial L}{\partial t} + \frac{\partial L}{\partial x}C \quad \ldots\ldots\ldots\ldots (1$$

This change can also be found from the rate at which the wave "stretches" due to the difference in velocity of two adjoining crests:

$$\frac{dL}{dt} = \frac{\partial C}{\partial x}L \quad \ldots\ldots\ldots\ldots (2$$

Eliminating the total derivative between (1) and (2) gives the following important relationshi

$$\frac{\partial L}{\partial t} + \frac{\partial L}{\partial x}C = \frac{\partial C}{\partial x}L \quad \ldots\ldots\ldots\ldots (3$$

We shall be concerned in general with the case where the wave velocity depends on wave len L and depth h only, or

$$C = C(L, h) \quad \ldots\ldots\ldots\ldots (4$$

where L = L(x, t), and the bottom profile along the path of travel is given by h = h(x).

Substituting the identity

$$\partial C/\partial x = (\partial C/\partial L)(\partial L/\partial x) + (\partial C/\partial h)(dh/dx) \quad \ldots\ldots\ldots\ldots (5$$

into (3) gives

$$\partial L/\partial t + [C - L(\partial C/\partial L)]\partial L/\partial x = (\partial C/\partial h)(dh/dx)L \quad \ldots\ldots\ldots\ldots (6$$

If V_L is defined by the equation

$$\partial L/\partial t + (\partial L/\partial x)V_L = 0 \quad \ldots\ldots\ldots\ldots (7$$

then to an observer traveling at velocity V_L the wave length remains constant. According to (6) and (7)

$$V_L = C - L(\partial C/\partial L) - L(dh/dx)[(\partial C/\partial h)/(\partial L/\partial x)] \quad \ldots\ldots\ldots\ldots (8$$

For the special case of constant depth, dh/dx = 0, and the partial derivative can be replaced a total derivative

$$V_L' = C - L(dC/dL) \quad \ldots\ldots\ldots\ldots (9$$

The V has been primed to denote the case of constant depth.

Equation (9) represents the well-known equation for group velocity at constant depth, and fo this special case has been derived by LAMB [1932, pp. 384-394] in a somewhat similar manner. ROSSBY [1945] derives (9) by equating the rate of increase of wave crests within a certain distan Δx to the excess of waves entering at x over those leaving at x + Δx. In analogy with the proble in hydrodynamics he uses the very descriptive term "wave continuity equation." Rossby also generalizes (9) to include some of our results.

These derivations identify the physical meaning of the term group velocity with the velocity the locus of a point in whose immediate vicinity the wave length remains constant. The same eq tion is usually derived from the interference pattern between two wave systems of equal amplitu and slightly different wave length, but that approach is unnecessarily restricted. The only assum tion which has been made here is that the waves are "conservative," that is, that individual cres maintain their identity.

Changes in wave period--Wave length, velocity, and period are related by the identity

$$L = CT \quad \ldots\ldots\ldots\ldots (10)$$

which permits restating the fundamental law (3) in terms of T and C rather than L and C:

$$C(\partial T/\partial t) + T(\partial C/\partial t) + [C(\partial T/\partial x) + T(\partial C/\partial x)]C = (\partial C/\partial x)CT$$

or

$$\partial T/\partial t + (T/C)(\partial C/\partial t) + C(\partial T/\partial x) = 0 \quad \ldots\ldots\ldots\ldots (11)$$

For the general case assume, as before

$$C = C(T, h),\ h = h(x) \tag{12}$$

efore, $\partial C/\partial t = (\partial C/\partial T)(\partial T/\partial t)$, and (11) becomes

$$\partial T/\partial t + \left\{ C/[1 + (T/C)(\partial C/\partial T)] \right\} (\partial T/\partial x) = 0 \tag{13}$$

To an observer traveling at a velocity

$$V_T = C/[1 + (T/C)(\partial C/\partial T)] \tag{14}$$

vave period remains constant. It is remarkable that the bottom slope does not enter explicitly the expression for V_T as it did for V_L, so that, in general, $V_T \neq V_L$. It is simpler to deal wave period than wave length, because then the equations are the same for the cases of con- and variable depth, or, by our previous notation

$$V_T' = V_T = V_L' \tag{15}$$

l subsequent equations V_T will be denoted simply by V and referred to as the group velocity.

The wave period of any system of waves in which the crests retain their identity must satisfy 'equation of continuity'' (13). Writing this equation in the abbreviated form

$$\partial T/\partial t + V(\partial T/\partial x) = 0 \tag{16}$$

olution can be put down at once:

$$T = T[t - \int (1/V)dx] \tag{17}$$

It is not possible to solve for the period explicitly, at least not in the general case, since T is ined in V and thus appears on both sides of the equation. As far as the integration is coned, on the other hand, V can be considered a function of h, or of x only, and

$$\partial T/\partial t = \partial T/ \left\{ \partial[t - \int (1/V)dx] \right\} \qquad (\partial T/\partial x) = \partial T/ \left\{ \partial[t - \int (1/V)dx] \right\} (-1/V) \tag{18}$$

n be seen that (17) satisfies the differential equation (16). The limits of integration in (17) are termined as yet, because no provisions have been made to fix the coordinate system. In most s it is convenient to let $t = 0$, $x = 0$, designate the time and position of the initial wave genera- If it were possible to measure a period T_o at or very near the origin, then according to the going convention $T_o = T(0)$.

Equations (16) and (17) define the ''field'' of wave period in the xt plane, and will be called equations. By applying the field solution (17) to problems dealing with tsunamis and swell re restrictions are imposed upon the dependence of period on distance x and time t. It will be n that these restrictions lead to results in agreement with observations.

In many problems it is more convenient to express the relationships in terms of individual s. For each individual wave the ''travel-time'' curve, $x = x(t)$, is fixed, and the transforma- from the field equations to the individual wave equation requires a line integral in the xt plane.

Equations for individual waves--To derive changes in period for individual waves, (16) can be oined with either of the equations

$$dT/dt = \partial T/\partial t + (\partial T/\partial x)C \qquad dT/dx = \partial T/\partial x + (\partial T/\partial t)(1/C) \tag{19}$$

ve the following sets of relationships:

$$\frac{dT}{dt} = -\left(\frac{C}{V} - 1\right)\frac{\partial T}{\partial t} = (C - V)\frac{\partial T}{\partial x} \tag{20 a, b}$$

$$\frac{dT}{dx} = -\left(\frac{1}{V} - \frac{1}{C}\right)\frac{\partial T}{\partial t} = \left(1 - \frac{V}{C}\right)\frac{\partial T}{\partial x} \tag{21 a, b}$$

The significance of the total and partial derivatives must be kept in mind: The partial deriva- refer either to changes with distance at a given instant, $\partial T/\partial x$; or changes with time at a location, $\partial T/\partial t$. The variables x and t are independent.

The total derivatives refer to changes of an individual wave which has traveled a distance x in ne t since it has been generated. For individual waves x and t are not independent. Indeed they related by (12) and (17):

$$C = C(T, x) = C(x, t) \ldots\ldots\ldots\ldots\ldots\ldots \text{(2}$$

which together with the definition of wave velocity

$$C = dx/dt \ldots\ldots\ldots\ldots\ldots\ldots \text{(2}$$

make solutions of the type $t = t(x)$ possible.

This distance-travel relationship for individual waves can in turn be substituted into (17) tc give solutions of the form

$$T = T(x) \text{ or } T = T(t) \ldots\ldots\ldots\ldots\ldots\ldots \text{(2}$$

Equations (20) and (21) give the differential expression, (24) the integral expression, for th period of individual waves. The meaning of these very general remarks can best be illustrated with specific examples.

Application to tsunamis

Theory--For low waves in water of depth h the velocity is given by the equations

$$C^2 = \frac{gL}{2\pi} \tanh \frac{2\pi h}{L} \ldots\ldots\ldots\ldots\ldots\ldots \text{(2}$$

or

$$C = \frac{gT}{2\pi} \tanh \frac{2\pi h}{CT} \ldots\ldots\ldots\ldots\ldots\ldots \text{(2}$$

Equations (25) were originally derived for an infinitely long wave train of constant period, but i has been shown by Cauchy and Poisson [LAMB, 1932] that they apply also to a wave system of gradually varying period. It has been customary to state that in very shallow water, that is, wa where

$$h < 0.05L \ldots\ldots\ldots\ldots\ldots\ldots \text{(}$$

(25) reduces to the well-known form

$$C^2 = gh \equiv C_o^2 \ldots\ldots\ldots\ldots\ldots\ldots \text{(}$$

according to which the velocity depends upon depth only, and the propagation is therefore non-dispersive.

Condition (26) is certainly fulfilled by all known tsunamis, and accordingly (27) has been a plied for computing travel times. These attempts have been remarkably successful.

There are, however, certain secondary phenomena associated with the propagation over lo distances, such as a very gradual increase in wave period, for which (27) is no longer a satisfa tory approximation. The first two terms in the expansion of a hyperbolic tangent are

$$\tanh\alpha = \alpha - (\alpha^2)/3 \ldots\ldots\ldots\ldots\ldots\ldots \text{(}$$

and to the same degree of approximation (27) becomes

$$C^2 = C_o^2[1 - (\alpha^2)/3] \ldots\ldots\ldots\ldots\ldots\ldots$$

where

$$\alpha = 2\pi h/L = 2\pi h/CT \ldots\ldots\ldots\ldots\ldots\ldots$$

For small values of α^2

$$\sqrt{1 - (\alpha^2)/3} = 1 - (\alpha^2)/6 \qquad 1/[1 - (\alpha^2)/6] = 1 + (\alpha^2)/6 \ldots\ldots\ldots$$

and

$$(C_o - C)/C_o = (\alpha^2)/6 \ldots\ldots\ldots\ldots\ldots\ldots$$

Percentage differences in the velocity of very long waves are therefore of the order of α^2. Tl rotation of the Earth also introduces dispersion, and for tsunamis of half-hour period or longe this effect cannot be neglected. But in the case of the short-period tsunami of April 1, 1946, t Earth's rotation increases the total dispersion by less than one per cent.

Differentiating (25b) gives

$$\partial C/\partial T = (g/2\pi)\left\{(\tanh\alpha - \alpha\,\mathrm{sech}^2\alpha)/[1 + (C_o{}^2/C^2)\,\mathrm{sech}^2\alpha]\right\} \quad \ldots\ldots\ldots\ldots (33)$$

can, in view of (29) and the expansion

$$\mathrm{sech}\alpha = 1 - (\alpha^2)/2, \ \mathrm{sech}^2\alpha = 1 - \alpha^2 \quad \ldots\ldots\ldots\ldots (34)$$

duced to the following form:

$$\partial C/\partial T = g(\alpha^3)/6\pi \quad \ldots\ldots\ldots\ldots (35)$$

Substituting into (14) gives

$$V = C_o[1 - (\alpha^2)/2] \quad \ldots\ldots\ldots\ldots (36)$$

terms of percentage differences

$$(C - V)/C_o = (\alpha^2)/3 \quad \ldots\ldots\ldots\ldots (37)$$

A comparison with (32) leads to the interesting result

$$C - V = 2(C_o - C) \quad \ldots\ldots\ldots\ldots (38)$$

at for any given wave period the group velocity is smaller than the wave velocity by twice mount that the wave velocity is smaller than the velocity of infinitely long waves.

Substituting (36) into (20) and (21) gives the following relationships for the changes in period dividual waves.

$$\frac{dT}{dT} = -\frac{\alpha^2}{3}\,\frac{\partial T}{\partial T} = \frac{\alpha^2}{3}C_o\,\frac{\partial T}{\partial x} \quad \ldots\ldots\ldots\ldots (39\text{ a, b})$$

$$\frac{dT}{dx} = -\frac{\alpha^2}{3}\,\frac{1}{C_o}\,\frac{\partial T}{\partial t} = \frac{\alpha^2}{3}\,\frac{\partial T}{\partial x} \quad \ldots\ldots\ldots\ldots (40\text{ a, b})$$

The general integral (17) can now be written in the form

$$T = T(t - t_o - I/T^2) \quad \ldots\ldots\ldots\ldots (41)$$

e

$$t_o = (1/\sqrt{g})\int h^{-1/2}dx \qquad I = (2\pi^2/g^{3/2})\int h^{1/2}dx \quad \ldots\ldots\ldots\ldots (42)$$

bottom profile along the path of travel is approximated by n short straight line segments, x_o, h_o to x_1, h_1; from x_1, h_1 to x_2, h_2; . . . , from x_{n-1}, h_{n-1} to x_n, h_n, then in the in-l (i - 1) to i

$$h = h_{i-1} + \frac{h_i - h_{i-1}}{x_i - x_{i-1}}(x - x_{i-1}) \quad \ldots\ldots\ldots\ldots (43)$$

42) can be integrated along each line segment:

$$= \frac{2}{\sqrt{g}}\sum_{i=1}^{n}\frac{1}{\sqrt{h_i} + \sqrt{h_{i-1}}}(x_i - x_{i-1}), \qquad I = \frac{4\pi^2}{3g^{3/2}}\sum_{i=1}^{n}\frac{h_i + \sqrt{h_i h_{i-1}} + h_{i-1}}{\sqrt{h_i} + \sqrt{h_{i-1}}}(x_i - x_{i-1}). \quad (44)$$

bulating corresponding values of h_i, x_i the integrals can be evaluated fairly rapidly.

The travel time t_o of an infinitely long wave can be computed according to

$$t_o = \int(1/C_o)dx \quad \ldots\ldots\ldots\ldots (45)$$

tting $\Delta t = t - t_o$, (41) can be written in the more convenient form

$$T = T(\Delta t - I/T^2) \quad \ldots\ldots\ldots\ldots (46)$$

first arrival of the tsunami is clearly indicated on the record, and if the initial wave period eds ten minutes, Δt may, with sufficient approximation, be taken as the time interval after the recorded arrival of the tsunami at a given station.

One particular form of the solution (46), and one that satisfies dimensional considerations, is

$$T = (1/a)(\Delta t - I/T^2) \quad \ldots\ldots\ldots\ldots (47)$$

e a is an arbitrary constant. Equation (47) represents a cubic equation in T, Figure 4A gives the relationship of period with time at the five selected stations. The relatively short periods of the tsunami of April 1, 1943, interference between waves traveling over different paths, and the superposition of seiches greatly reduce the accuracy with which periods can be measured. Certain portions of the records at San Luis Obispo and La Jolla had to be omitted because of severe seiche formation. At Honolulu a three-minute seiche is predominant after the first hour, and the measured periods from the nearby Waima River water-stage recorde have been taken into account in drawing the curve. It would be desirable to apply more refined methods of period analysis, but these are made difficult by the slow recording speed (one hour = one inch) and the resulting extreme vertical exaggeration of the record.

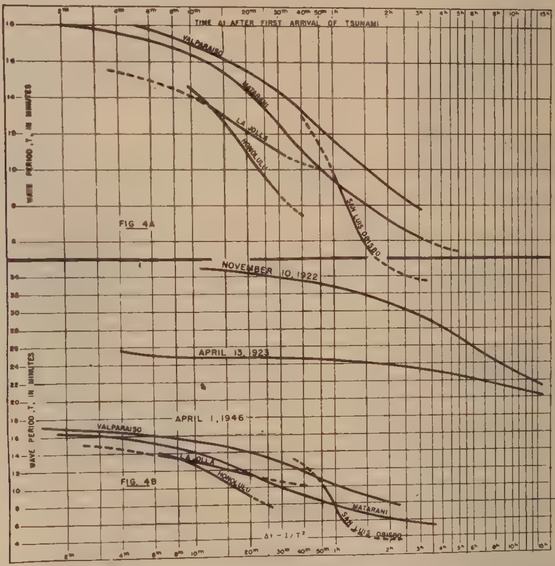


Fig. 4--A, period against time of April 1, 1946, tsunami at various stations; B, plot of general solution (17) for three different earthquakes

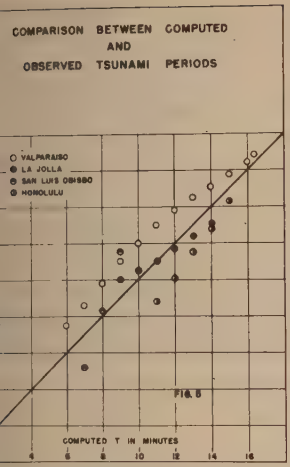
Comparison between theory and observations--The observed field of wave period is in quali tative agreement with the theoretical considerations. The period increases with distance of travel, but decreases with time at every given station.

For a quantitative check, corresponding values of T, Δt (see Fig. 4A), and I (see Table 1) were substituted in the general field solution (46) and plotted in Figure 4B.

In accordance with the theory all observations pertaining to the tsunami of April 1, 1946, fr Hawaii to Chile, obey the same general relationship, while observations of the two other tsunam follow a different relationship. Thus the indeterminateness of the function in the general solutio (46) depends upon the nature of the original disturbance. Preliminary considerations indicate t long periods in Figure 4B indicate a large horizontal extent of the initial disturbance. Perhaps the size and shape of the initial disturbance could be estimated by assuming certain forms of th initial deformation, or initial impulse, for which an analysis of the Cauchy-Poisson type can be carried through, and then constructing a network of lines on Figure 4B corresponding to variou types and sizes of the initial boundary conditions. A comparison of this network with observed relationships, such as the ones in Figure 4B, may yield information regarding the nature and si of the original disturbances.

A feature which is obscured by the logarithmic scale of the abscissa is that the leading wav especially the portion of the wave preceding the first crest, is associated with small values of $\Delta t - I/T^2$, and large values of T. Therefore a in (47) must be small and the approximate solutio (50) is applicable, so that the periods of the very first waves, the "forerunners" are approxima proportional to $\sqrt{I}$ and inversely proportional to $\sqrt{t}$.

From any one complete record it is possible to compute the periods at any of the other sta Assuming the Matarani record to define the relationship for the tsunami of April 1, 1946, the periods for all other stations have been computed for various values of Δt, and plotted against the observed periods (see Fig. 5). The observed wave periods in the North Pacific tend to be somewhat shorter, those at Valparaiso longer than the computed periods. The same conclusion follows directly from (40a), which gives an average increase in the period of the first wave of 1.3 minutes in 5000 miles. GREEN [1946] has measured the time interval between the first crest and first trough and on that basis estimates the period increase of the first wave to amount to 2.0 minutes in 5000 miles. The observational data are too inaccurate to determine whether this discrepancy is significant, and whether it therefore indicates a more rapid increase in period than the increase due to dispersion. ("... the amount of increase in period is difficult to determine from the present records. For instance the table shown in my paper indicates an increase of around two minutes. But by dropping the shortest period station from the California group, and the longest period station from the Peru-Chile group, the mean value of increase in period would be 1-1/3 minutes from California to South America." [C. K. Green, July 18, 1946, personal communication to the author])



g. 5--Computed wave periods based upon (17) and the observed periods at Matarani, Peru

Application to swell

Theory--For low waves in deep water, the velocity depends upon wave length alone, or period alone,

$$C = \sqrt{gL/2\pi} = gT/2\pi \quad \text{.......................} \quad (51)$$

he following formulae are therefore much simpler than in the case of tsunamis. Equations nd (14) lead at once to the well-known relationships

$$V_T = V_L = V = C/2 \quad \text{........................} \quad (52)$$

tions (20) and (21) give

$$\frac{dT}{dt} = -\frac{\partial T}{\partial t} = \frac{C}{2}\frac{\partial T}{\partial x} \qquad \frac{dT}{dx} = -\frac{1}{C}\frac{\partial T}{\partial t} = \frac{1}{2}\frac{\partial T}{\partial x} \quad \text{..............} \quad (53)$$

tion (17) reduces to

$$T = T(t - \sigma x/T) \text{........................} \quad (54)$$

e $\sigma = 4\pi/g$ (dimensions t^2/L). The integral (54) has been given by ROSSBY [1945].

The special case corresponding to (47) gives

$$T = (t/2a)(I \pm u) \quad \text{........................} \quad (55)$$

e $u = \sqrt{1 - 4\pi ax/t^2}$; if, furthermore, a = 0 (50)

$$T = \sigma x/t \quad \text{..............................} \quad (56)$$

h is a solution of the Cauchy-Poisson wave problem [LAMB, 1932].

It will be shown that the special solution (56) is in good agreement with observations of the erunners" of swell from a distant storm. This is assumed to justify the use of the simple tion for all further derivations, though the agreement might also have been expected from the ogy with the forerunners of the tsunami. The following discussion deals therefore exclusively the forerunners, and is not applicable to the visible swell. Some of the following derivations d have been given for the general case, but the not inconsiderable difficulties involved in dealvith a moving source are greatly simplified by working with the special solution.

To derive the equations for individual waves, T can be eliminated between (51) and (56), t ≡ C = gT/2π = 2x/t. Integrating gives

$$x/x_D = (t/t_D)^2 \quad \text{.........................} \quad (57)$$

$$T/T_D = t/t_D = \sqrt{x/x_D} \tag{58}$$

$$\partial T/\partial t = -\sigma x/t^2 = -T/t \tag{59}$$

The subscript "D" may refer to any fixed point on the wave's journey, but will here be taken to denote conditions at the wave station. If T_D and $(\partial T/\partial t)_D$ are determined from the wave record, then the distance and time of travel can be computed from (59):

$$x_D = T_D^2/\sigma(-\partial T/\partial t)_D \qquad t_D = T_D/-(\partial T/\partial t)_D \tag{60 a, b}$$

Waves from a moving storm--Application of these equations to the study of swell is difficult, because one must deal with a moving source of finite size which continuously emits new waves. I will be assumed that the problem can be treated as one involving an infinite number of instantaneous sources, each independently emitting a wave field according to the assumptions made earlier. Let x and t retain their former meanings, designating the total distance and time, respectively, th any wave has traveled. The fixed coordinated system will be denoted by χ and τ, χ representing distance from the wave origin to the wave station, and τ the time on some standard scale, for example, GCT.

The movement of the storm center is represented by the equation

$$\chi_c = \phi(\tau) \tag{61}$$

Let $\delta\chi$ be the distance of a point of wave origin from the storm center, so that

$$\chi = \chi_c + \delta\chi \tag{62}$$

Waves arriving at the wave station at any time τ were generated at a time $\tau - t$ when the storm center was located at

$$\chi_c = \phi(\tau - t) \tag{63}$$

To determine the period at the wave station at a time τ, set $x = \chi = \phi(\tau - t) + \delta\chi$ and substitute into (56)

$$T = \sigma[\phi(\tau - t) + \delta\chi]/t \tag{64}$$

At any time τ a spectrum of wave periods must be present at the wave station, because of two factors: (a) Waves arrive simultaneously from different sectors of the storm (different value of $\delta\chi$); and (b) waves arrive simultaneously, although they were generated at different times (different values of t).

The total width of the period "band" is given by

$$\Delta T_\tau = [\partial T/\partial(\delta\chi)]F + (\partial T/\partial t)Q \tag{65}$$

where F is the effective length of the storm fetch at a time $(\tau - t)$, and Q is the time interval during which waves perceptible at the station were generated. Partial differentiation of (64) lead to the expressions

$$[\partial T/\partial(\delta\chi)]F = \sigma F/t, \quad (\partial T/\partial t)Q = -(\sigma/t)(V - U)Q \tag{66 a, b}$$

where

$$U = -[\partial\phi/\partial(\tau - t)] \tag{67}$$

is rate of the storm movement towards the wave station at the time $(\tau - t)$, and $V = \chi/t$ the group velocity.

Equations (66) may also be interpreted to give the width in the period band due to the instantaneous actions of a finite storm (66a), and due to a moving point source (66b), respectively. The longest periods in the band are those of the earliest perceptible waves from the furthest sector o the storm; the shortest periods are due to the waves generated latest near the leading edge of the storm.

The shift in period of the band as a whole will be interpreted with the aid of an actual examp It will be shown that the shift is related to the position and speed of the storm, and can therefore provide clues regarding changes in the meteorological situation. The width and appearance of th band should provide some information about the size and character of the storm itself.

Observations--Unfortunately no simultaneous wave records from two or more well-separated
ions are available to test the theory. The proposed wave recording stations at La Jolla, Cali-
ia, and San Nicolas Island, 120 miles west-northwest from La Jolla can be expected to give
able information. Observation shows that the increase in swell period for an individual wave
be of the order of two seconds a day [SVERDRUP and MUNK, in press]. According to (53),
an average period of ten seconds, $\partial T/\partial t = -2$ sec/day $= -2.3 \times 10^{-5}$ sec/sec; $\partial T/\partial x =$
4×10^{-6} sec/ft $= 6 \times 10^{-3}$ sec/naut mi. The corresponding period difference over 120 miles
bout 0.7 second. Both $\partial T/\partial t$ and $\partial T/\partial x$ can therefore be measured with existing instruments.
parison of the observation with the foregoing considerations would show whether the assump-
s made in this report are applicable to swell, and especially whether the significant waves,
is, the highest waves present, and the ones that determine the character of the surf, maintain
r identity.

Some confirmation of the applicability of the theory to a long swell can be found in records
n a single wave station at Pendeen, England. (The Oceanographic Research Group, Admiralty
earch Laboratory, Teddington, England, have kindly placed at our disposal unpublished records
well at Pendeen, near Lands End.) The waves were measured by means of a differential pres-
e recorder on the ocean bottom at an average depth of 114 feet. The records were then ana-
ed for period by a frequency analyzer, specially designed for that purpose at the Admiralty Re-
rch Laboratory.

Figure 6 shows a set of period analyses of 20-minute records taken at intervals of two hours.
abscissa give simply wave periods in seconds, but the ordinates are more difficult to inter-
t, depending both upon the frequency of occurrence of a certain period, and upon the corre-
nding wave height.

The band of gradually diminishing periods in Figure 6 is the result of an intense cyclone
ch formed off the coast of Cuba, 3000 miles from Pendeen, on March 10, 1945, and traveled in
neral northeasterly direction, passing west of the British Isles. The positions of the forward
rear edges of the storm are given in Figure 7A. These were determined from six-hourly
ther maps, following the rules for measuring fetches for wave forecasting [UNITED STATES
ROGRAPHIC OFFICE, 1944]. Four representative weather maps are included in Figure 7.
weather maps were drawn and analyzed at the United States Navy Weather Central, Washing-
D. C.

The first indications of the storm on the wave record are some "low-frequency noises" at
00^{m} GCT, March 14, 1946. At that time visual observations at Pendeen noted only the presence
en- to 12-second waves from local winds. The long "forerunners" of the swell were too low
e visible. The upper and lower limits of the period band have been read off the record and
wn on Figure 7B to emphasize the similarity between the recorded wave periods and the ob-
ved storm paths. A relationship between the width of the period band and the fetch is also
arent. The implications of (64) - (66) are therefore borne out by the observations. It will be
wn, however, that the similarity of the curves in Figure 7 may be misleading, and that great
e must be exercised in the interpretation of the wave records.

Comparison between theory and observations--We shall first deal with the lower boundary of
period band. The initial waves from the storm of March 10 to 13, 1946, reached Pendeen
nd $16^{h}00^{m}$, March 14, 1946, with a minimum period of 19 seconds. Let this time and period
esignated by τ_0 and T_{τ_0}, and let X_0 and $\tau_0 - t_0$ refer to the distance from Pendeen and the
e of wave origin. Then the period recorded at time τ_0 equals:

$$T_{\tau_0} = \sigma X_0/t_0 \quad \text{(68)}$$

Assume that the "instantaneous" disturbance which gave rise to the waves described in (68)
the only existing source of the waves present; then slower waves with shorter periods would
ow the faster longer waves, so that the period at the wave station would decrease with time
ording to the equation

$$T_{\tau} = \sigma X_0/t \quad \text{(69)}$$

re $(\tau - t) = (\tau_0 - t_0)$ is the time of the disturbance. Therefore, as long as the lower limit of
band is defined by the waves from a single instantaneous disturbance,

$$\partial T/\partial \tau = \partial T/\partial t \quad \text{(70)}$$

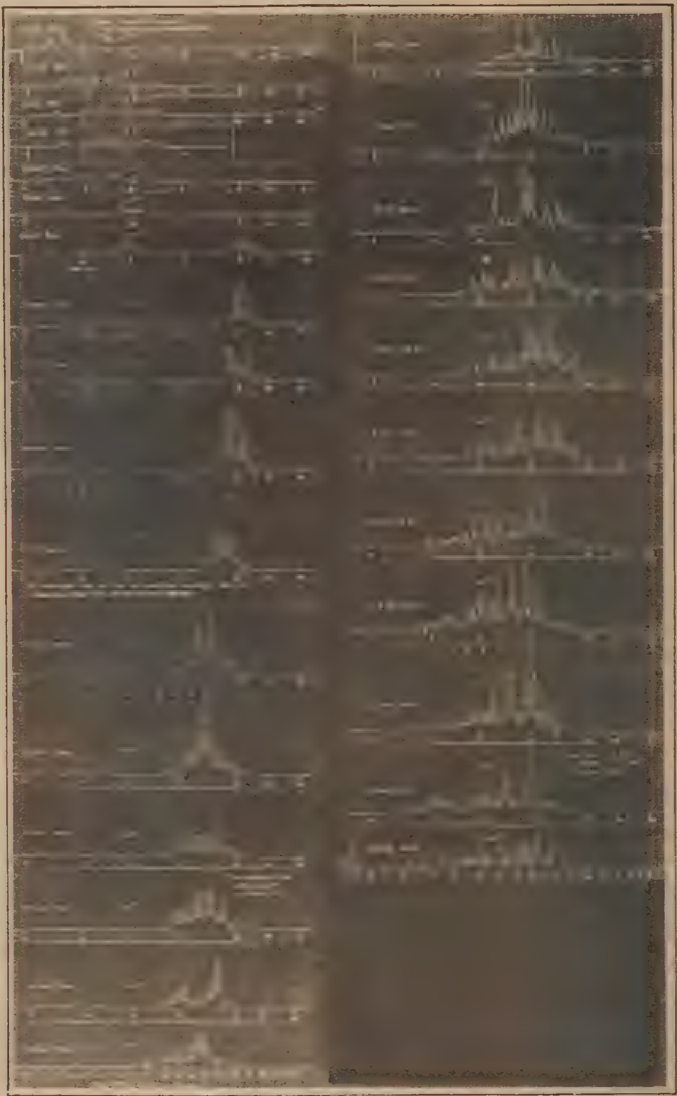


Fig. 6--Spectogram of waves at Pendeen, England, at two-hour intervals from March 14, 1946, 04^h00^m to March 16, 1946, 12^h00^m

Let another instantaneous disturbance at a time $\tau - t + \Delta\tau$ and distance $\chi' = \chi - \Delta\chi$ generate a system of waves which arrives at Pendeen simultaneously with the first system, thus having traveled a time interval $t' = t - \Delta\tau$. The period of waves from the second disturbance at time τ equals $T_\tau' = \sigma(\chi - \Delta\chi)/(t - \Delta\tau)$, and

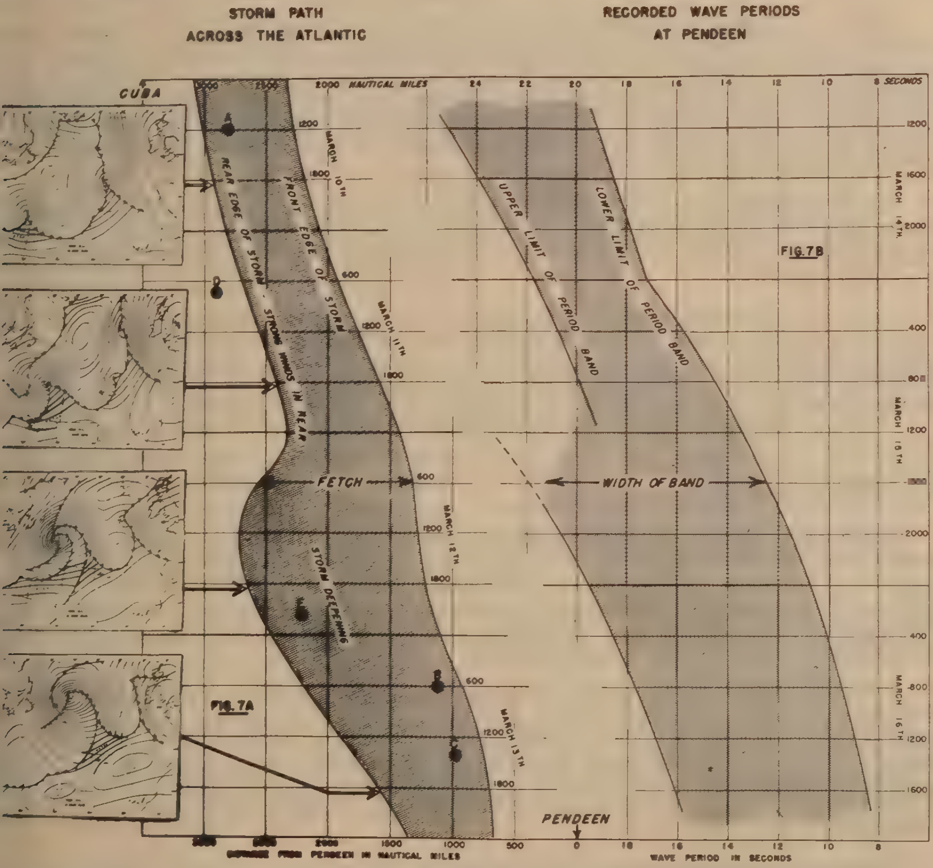
$$T_\tau' - T_\tau = \frac{\sigma}{(t - \Delta\tau)}\left(\frac{\chi}{t} - \frac{\Delta\chi}{\Delta t}\right)\Delta\tau \quad \ldots\ldots\ldots\ldots\ldots\ldots (71)$$

As the time and distance between the two disturbances is decreased without limits, (71) approaches the differential equation (66b) for a moving point source. According to (51), (52), and (56

$$\chi/t = V = T/\sigma \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (72)$$

$$\Delta\chi/\Delta t = \overline{U} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (73)$$

be considered the average velocity of the storm movement between any two points. Therefore,
is higher than, equal to, or lower than T according to whether V is larger than, equal to, or
aller than $\overline{U}$. For T = 19 seconds, V = 29 knots, while $\overline{U}$ during the first day of storm was
ut 17 knots. Since the forerunners of the swell travel at considerable speed, the initial de-
ase of the lower limit of the band results from the characteristics of a single wave system
m the earliest perceptible disturbance, and is therefore similar to the decrease of the tsunami
iod at a fixed station. The time and position of the origin of this wave system can be plotted as
oint in Figure 8A, where it should fall within the observed storm track. The point will be called
"focus" of a certain portion of the wave-band boundary. The circles in Figure 8 give the
er limits of the period band, as they were measured on the Pendeen record. The position of
focus is computed in the following manner: (1) At the time τ = March 14, 1946, 18^h00^m, Figure
nows T = 18.2 seconds, $\partial T/\partial\tau = -0.18$ sec/hr; (2) Equations (70) and (60) give χ = 2800 naut mi,
102 hr; (3) March 14, 1946, 18^h00^m minus 102 hours is March 10, 1946, 12^h00^m. The position
he focus is shown by the large circle marked A in Figure 7A, and falls well within the observed
rm track; (4) Setting χ_0 = 2800, and τ = March 10, 1946, 12^h00^m + t in (69) plot T_τ for various
ues of t in Figure 8.


STORM PATH ACROSS THE ATLANTIC

RECORDED WAVE PERIODS AT PENDEEN

Fig. 7--Storm path across Atlantic, showing similarity in appearance to recorded wave periods at Pendeen. Points A--E in Figure 7A are locations of wave origin computed from wave records, suggesting possibility of using wave observations for tracking storms

$$1/C = T\int_T^{\infty}(1/VT^2)dT \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots ($$

The rate of period increase of an individual wave

$$\frac{dT}{dx} = \left(\frac{1}{V} - \frac{1}{C}\right)\left(-\frac{\partial T}{\partial t}\right) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2$$

can now be computed from (74), the empirical relationship V = V(T), and the measured decreas period with time at a given station.

General observations--MACELWANE [1923], who also made the problem of period increas the subject of his doctor's dissertation, obtained an average value of $dT/dx = 1.4 \times 10^{-8}$ sec/c for the California earthquake of January 31, 1922. This figure represents the increase in peri of waves occurring two and four minutes after the first arrival of surface waves, and this incre must be somewhat larger than the corresponding increase of individual waves. GUTENBERG [1939] suggests an equation of the form

$$T^2 = T_0^2 + ax/V^3 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots ($$

for the period increase of an individual wave, and gives a value of $a \approx 10^{10}\,\mathrm{cm}^2/\mathrm{sec}$ for seismi surface waves. For various values of T, and corresponding values of V [GUTENBERG and RIC TER, Fig. 1, 1936] (75) gives the values shown in Table 2. The cauda of the surface waves inc in period at the rate of $dT/dx = 1.4 \times 10^{-8}$ sec/cm [GUTEN BERG and RICHTER, Fig. 5, 1936]. BYERLY [1926] has m a careful study of the Montana earthquake of June 28, 1925, his data indicates dT/dx to lie between 1.4×10^{-8} and 1.8 10^{-8} sec/cm.

Table 2--Values of T and corresponding values of V

T	V	dT/dx
sec	km/sec	sec/cm
10	3.45	1.2×10^{-8}
15	3.45	0.8×10^{-8}
20	3.5	0.6×10^{-8}
25	3.6	0.4×10^{-8}

All these estimates deal with long distance propagation from major shocks, and they consistently lead to an increa of the order of one second per 1000 km. To compare this value with theory the clearest records from American stat (Pasadena, Lick, Berkeley, and St. Louis) have been selec from Byerly's report on the Montana earthquake [BYERLY, 1926], and the average relationship between period and time plotted in Figure 10D. The relatic ship V = V(T) is again taken from Figure 1, GUTENBERG and RICHTER [1936], and the wave velocity shown in Table 3 is found by numerical integration of (74). The computed and observ period increases are therefore of the same order of magnitude.

Table 3--Numerical integration of (74)

T	V	C (74)	∂T/∂t (Fig. 10D)	dT/dx
sec	km/sec	km/sec	sec/sec	sec/cm
10	3.56	3.76	0.058	0.9×10^{-8}
12	3.52	3.80	0.110	2.3×10^{-8}
14	3.50	3.85	0.18	4.8×10^{-8}

The Mexican earthquake, February 22, 1943--Figure 10A shows records of this shock at t various stations maintained by the Pasadena Seismological Laboratory. C. F. Richter of the S mological Laboratory, Pasadena, has gone to considerable trouble in selecting a set of recorc suitable for this discussion. Tracing individual waves from station to station by making use o known distances and wave velocities has been attempted, but the identification, which is difficu especially for the furthest station, is not essential to the following analysis.

Figure 10B shows the relationship between period and time at the four stations. Figure 1 is a plot of the basic solution (17) provided that the transmission characteristics are uniform the x direction, so that

$$T = T(t - x/V) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

where t is time (GCT), V is the group velocity, and x is the excess of the travel distance over distance to La Jolla. The theory is confirmed by the fact that observations for the four statio obey a single relationship. The procedure is analogous to the one followed earlier in the anal of the tsunami of April 1, 1946. The similarity between the curves in Figures 4B and 10C is striking and suggests the possibility that the nature of the general solution (76) may serve as means of estimating the horizontal extent of the initial seismic disturbance.

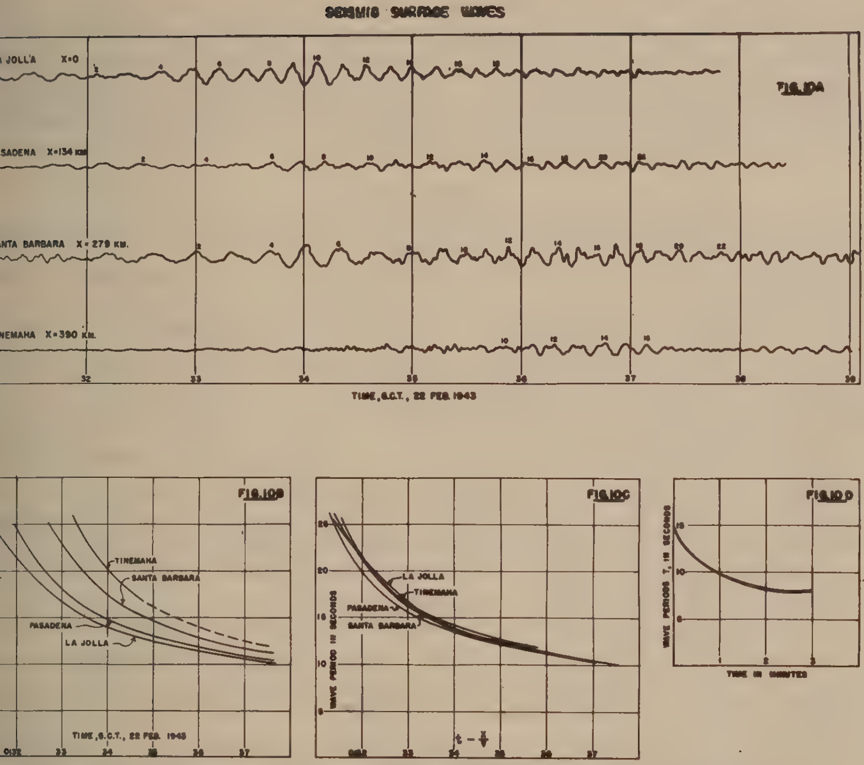


Fig. 10--A, records of Mexican shock at four Southern California stations; B and D, period against time for the Montana and Mexican earthquakes, respectively; C, general solution (76) for the Mexican earthquake

nclusions--The theory for the increase in wave period leads to two expressions which are ally suitable for comparison with observations. The differential form

$$\frac{dT}{dx} = \left(\frac{1}{V} - \frac{1}{C}\right)\left(-\frac{\partial T}{\partial t}\right) \ldots\ldots\ldots\ldots\ldots\ldots \quad (21a)$$

he period increase with distance of an individual wave of group velocity V, wave velocity C, e of period decrease at a fixed point $\partial T/\partial t$. Between two stations separated by a finite e average values have to be used. The integrated form for the wave field requires that single disturbance all waves at any time t and distance x must obey the same functional nship

$$T = T[t - \int (1/V)dx] \ldots\ldots\ldots\ldots\ldots\ldots \quad (17)$$

th forms have been applied successfully to the examples in this report. However, each tion poses its own particular problem. For the tsunami the variation in depth along the travel must be taken into account. In the case of the forerunners of the swell, complexities ted with a moving continuous source must be considered. For the seismic surface waves persion relationship must be taken from empirical evidence.

t in spite of the fact that we have dealt with different geophysical phenomena the increase od seems to follow the same physical law. The nature of the functional relationship in (17) kingly similar for the tsunami and the seismic surface waves. In all instances the period se is slow except for the leading waves, whose periods are approximately proportional to avel time and to the square root of their travel distance. From the experience gained it likely that other phenomena dealing with long-distance wave propagation can be brought e same theoretical framework.

Acknowledgments--The assistance of various agencies and persons has been acknowledged at appropriate places in the text. I am especially indebted to C. K. Green, United States Coast and Geodetic Survey, and B. Gutenberg and C. F. Richter of the Seismological Laboratory, California Institute of Technology. Robert S. Arthur, U. S. N. R. has offered a number of suggestions, and C. J. Burke, A. A. F., has carefully read the manuscript and checked the mathematical equations. T. Saur, Jr. has helped with the computations. Although this is the first paper on waves which I have not written jointly with H. U. Sverdrup, the influence of his thinking pervades this investigati

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Scripps Institution of Oceanography,
University of California,
La Jolla, California

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Contribution No. 310

ATURAL HYBRIDS BETWEEN TWO SPECIES OF CATOSTOMID FISHES *

CARL L. HUBBS AND LAURA C. HUBBS

YBRIDIZATION in nature between species of *Catostomus* and
between species of that genus and those of *Pantosteus* is rela-
ly frequent throughout the western United States (Hubbs,
bbs, and Johnson, 1943).[1] Of the nine interspecific combinations
t have been discovered and described — ten if subspecies are
arately enumerated — the least adequately known is *Catostomus*
pinnis × *Pantosteus delphinus*. Of this species cross there has been
cribed only one specimen, so small (25 mm. in standard length) as
ast some doubt on the identification. Interest and satisfaction
refore attended our discovery, soon after the initial publication on
ostomid hybrids, of six additional specimens of this interspecific
ibination, representing a new subspecies cross, *Catostomus lati-*
nis discobolus × *Pantosteus delphinus delphinus*. All six specimens
e included in recent collections from the Colorado River drainage
Colorado.

METHODS

In this paper we follow the statistical methods, the mode of
sentation, and the criteria for the recognition of hybrids that were
posed in our 1943 report. Two procedures are added. First, we
w graphically for each measured character in each comparison
ain statistics for the parental species along with the actual pro-
tions of each hybrid specimen (Figs. 1–2). The statistics for the
ental forms are presented by a slight modification of the graphical

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[1] We take advantage of this opportunity to correct two annoying typo-
hical slips in the paper by Hubbs, Hubbs, and Johnson. On page 36, line 9,
"objections" read "objects," and on page 63, line 11, for "intraspecific"
"interspecific." In the discussion of the "character index" (pp. 4–6) we
vertently omitted reference to Van Denburgh's (1920) pioneering "summa-
of characters."

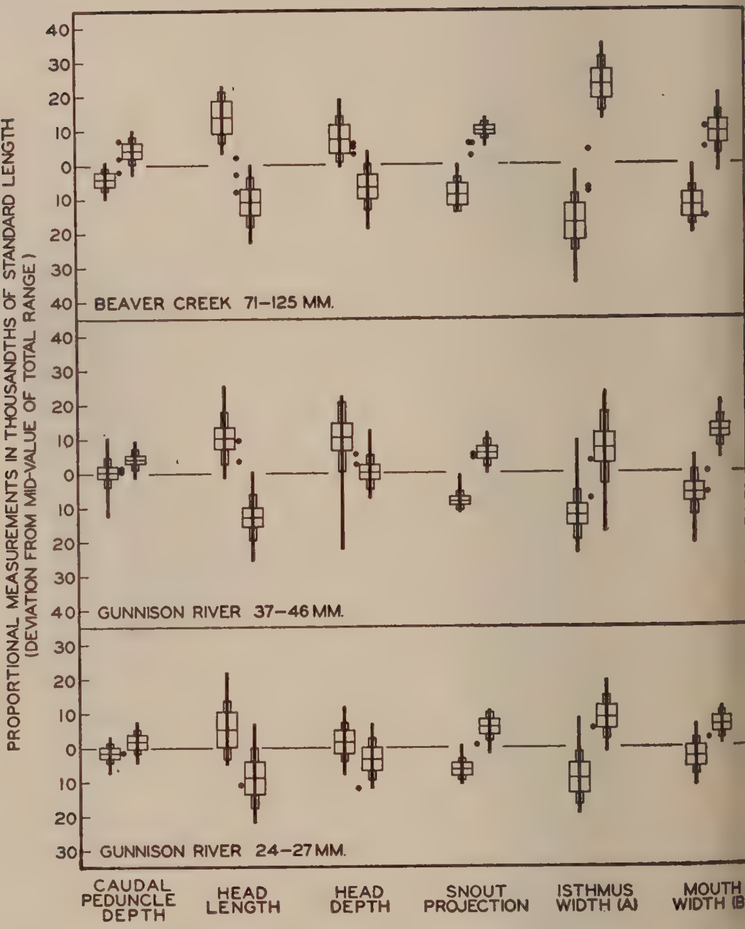
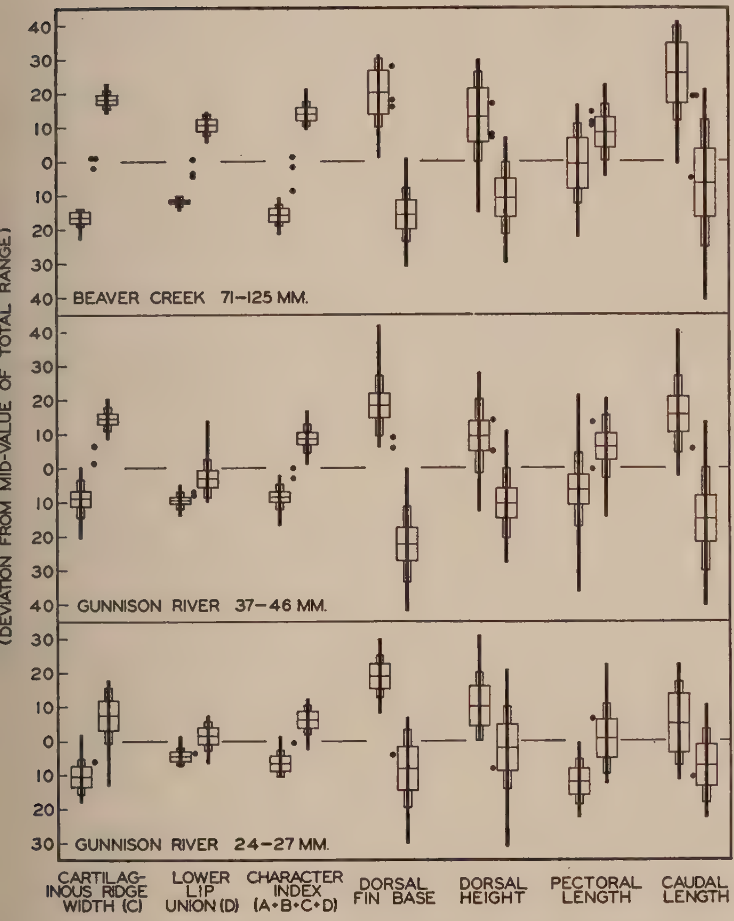


Fig. 1. Proportional measurements of the hybrids compared with those of th parental species, *Catostomus latipinnis discobolus* and *Pantosteus delphinu delphinus*, at three comparable size groups. Two collections are represented Actual values are given for the hybrids, statistical data for the two species

method of Dice and Leraas as refined by Hubbs and Perlmutte (1942): The standard deviation on either side of the mean is repre sented by a hollow vertical rectangle rather than by a black bar Secondly, we have computed, for each of the specimens of th



IG. 2. Proportional measurements of the hybrids and the parental species (*continued*). For each set of the two species there are given the observed range, the mean, one standard deviation on each side of the mean (as the vertical rectangle), and twice the standard error on each side of the mean (the horizontal rectangle)

arental species in one series (that from Beaver Creek) a figure cor-esponding to the hybrid index. The average index shows how well ach individual corresponds with its proper species and to what degree if any the parental forms and the hybrids overlap in the simple average summation of proportional measurements (see discussion on p. 164).

In making counts and measurements we follow the methods previously specified (Hubbs, Hubbs, and Johnson, 1943 : 3–4), with the exception that we take as the origin of the dorsal fin the actual base of the first ray and measure the height of the fin (from that point to the tip of the anterior lobe), rather than the depressed length of the fin. We add one character, snout projection. This is the amount that the snout projects beyond the anteriormost point on the upper lip, expressed in thousandths of the standard length. When the lip is the more anterior the value for snout projection is negative. The measurement was made under adequate magnification with precision dial calipers. First the tip of the lip was sighted below the square edge of one caliper arm, held at an approximate right angle with the axis of the fish; then the other arm was moved closer until the tip of the snout appeared directly below its edge; the interval was estimated to 0.01 mm. This is a valuable character for the recognition of the intergeneric hybrids, for in *Pantosteus* the snout projects more than it does in *Catostomus*. Previously, however, we have not attempted a quantitative measure, because the soft bulbous snout of suckers shrinks greatly in routine preservation. The new material, fortunately, was so little shriveled that the snout projection could be measured with considerable precision. The use of borax with the formalin prevented shrinkage of the Beaver Creek specimens, which were measured before they were transferred to alcohol. The young from Gunnison River were handled in alcohol, but were soft and little shrunken, apparently as the result of crowding during the original preservation in formalin.

ACKNOWLEDGMENTS

Dr. Reeve M. Bailey coöperated in this study by supplying specimens and data from the Museum of Zoology of the University of Michigan. Dr. John T. Greenbank, a former student, collected the young hybrids from Gunnison River, along with a large quantity of other valuable material. Research Assistant Elizabeth M. Kampa helped us collect the yearling hybrids in Beaver Creek, made the fin-ray counts for the parental species from this locality, painstakingly drew the two graphs, and rendered other assistance.

MATERIAL

All material dealt with in this as in our preceding report is eposited in the Museum of Zoology of the University of Michigan U.M.M.Z.).

Catostomus latipinnis discobolus × *Pantosteus delphinus delphinus*

U.M.M.Z., No. 142529: Three yearlings 80 to 105 mm. in standard length, ollected by the authors and Elizabeth M. Kampa in Beaver Creek, a tributary Los Pinos Creek in the San Juan River system, La Plata County, Colorado, Township 35 North, Range 6 West, on Trinchera Ranch, along U. S. Highway 60; October 10, 1944.

U.M.M.Z., No. 142917: Three young 25 to 43 mm. long, seined by John T. reenbank and party in a side channel then cut off from Gunnison River, at its unction with North Fork; October 20, 1943.

The material of the parental species used in the comparisons was eined with the hybrids, in numbers as indicated in the following ection.

RELATIVE NUMBERS OF HYBRIDS AND OF PARENTAL KINDS

Where the yearling hybrids (U.M.M.Z., No. 142529) were collected in Beaver Creek suckers were extremely numerous, and the ther fishes present, *Rhinichthys osculus yarrowi* and *Cottus bairdii unctulatus*, were common. In addition to young suckers and young lace that were discarded in the field, a total of 408 fish specimens was

TABLE I

RELATIVE NUMBERS OF *CATOSTOMUS LATIPINNIS DISCOBOLUS*, HYBRIDS, AND *PANTOSTEUS DELPHINUS DELPHINUS*

Specimens in University of Michigan Museum of Zoology	*Catostomus latipinnis discobolus*	Hybrids	*Pantosteus delphinus delphinus*
In collection containing hybrid			
U.M.M.Z., No. 142529	16 (6.3%)	3 (1.2%)	236 (92.5%)
U.M.M.Z., No. 142917	258 (23.4%)	3 (0.3%)	841 (76.3%)
Total	274 (20.2%)	6 (0.5%)	1,077 (79.4%)
From the Colorado River system	1,733 (33.8%)[1]	6 (0.1%)	3,381 (66.0%)[1]

[1] There may be a slight error in these numbers and percentages (see pp. 152, 160–162).

seined during one-half hour in a few seine hauls. The thick concentration of fish was attributable to the almost complete stair-stepping of the very small creek by innumerable beaver dams (according to Feast, 1944 : 1, ninety-five beaver were trapped during the winter of 1943–44 within the Trinchera Ranch, on which Beaver Creek is the water supply). Like the hundreds of other ponds, the one that was fished provided excellent room and shelter for the fish, for the water was several feet deep in the lower part of the pond and as much as twenty-five feet wide, and there was much brush in and over the water; the short stretch of gravelly current between the pond and the next dam upstream obviously afforded suitable spawning grounds.

It may be presumed, however, that the spawning fish must have been much crowded on the limited area of gravel. This is one of the circumstances that have appeared to be conducive to hybridization, for instance, in the Centrarchidae (Hubbs and Hubbs, 1932 : 428).

In the one beaver pond and short stretch of running water that was seined the two species of sucker were present in very unequal numbers (Table I). Along with the 3 yearling hybrids there were preserved 5 young and 11 half-grown of *Catostomus latipinnis discobolus* and 213 young and 23 half-grown to adult specimens of *Pantosteus delphinus delphinus*. Had the myriads of young suckers been saved, the recorded proportion of *Pantosteus* would obviously have been much higher. It is very probable that the conditions were relatively unfavorable for the *Catostomus*, which is ordinarily a fish of larger and swifter waters. Since so few of the young suckers were of this species it is probable that the local conditions were not very favorable for spawning. For the *Pantosteus*, in contrast, the situation seems to have approached the optimum. The occurrence of only a few of the *Catostomus* with such large numbers of the *Pantosteus* yielded two very different hybrid ratios; in the sample, relatively random except for the discarding of many young that were predominantly *Pantosteus*, the hybrids were 19 per cent as numerous as the *Catostomus* but only 1.3 per cent as many as the *Pantosteus*. It is unfortunate that the hybrids were not recognized in the hurried field collecting, because it would have been easy to collect a very large and more completely random sample for a more adequate analysis of the relative frequency of the hybrids, and also for a more thorough statistical comparison of their characters with those of the parental forms.

In Gunnison River also *Pantosteus delphinus delphinus* predomiated, but the disparity in numbers of the parental species was not so reat as in Beaver Creek (Table I). With the 3 young hybrids there ere seined 256 young and 2 yearlings of *Catostomus latipinnis discoolus* and 841 young (1 possibly a yearling) of the other species. ssociated fishes occurred in the same collection in the following umbers: *Catostomus commersonnii sucklii*, 27 young; hybrids, *C. c. ucklii* × *Pantosteus d. delphinus*, 9 young; *Rhinichthys osculus yarowi*, 19 young and yearlings; *Gila robusta robusta*, 14 young. The bundance of young fish at this locality suggests that there may have een some crowding of the adults on the spawning grounds, here as ell as in Beaver Creek.

In all probability *Catostomus latipinnis discobolus* and *Pantosteus elphinus delphinus* hybridize less frequently than do certain other airs of species in these genera (compare Table I of this paper with able XXXI in Hubbs, Hubbs, and Johnson, 1943 : 64). Many of he collections in the Museum of Zoology contain both species without ny crosses. The occurrence of three hybrids in the Beaver Creek eries may be attributed to the association of a few individuals of the *atostomus* with an abundance of the *Pantosteus*, and the factor of ifferential abundance may also have contributed to miscegenation n the Gunnison, though the disparity in numbers was apparently uch less in that stream. That the cohabitation of a rare and an bundant species is conducive to natural hybridization is suggested by ome of the data given for suckers by Hubbs, Hubbs, and Johnson nd is more definitely indicated by the known information on hyridization in nature between species of Cyprinodontidae (Hubbs, alker, and Johnson, 1943). Other data confirm the hypothesis.

The evidence (p. 152) that *Pantosteus delphinus delphinus* in unnison River had crossed more commonly with the introduced *atostomus commersonnii sucklii* than with the native *C. latipinnis iscobolus* falls in line with the theory that hybridization rates may be ncreased when exotic and indigenous species meet. Since the conlusions by Hubbs, Hubbs, and Johnson (1943 : 12–14, 39, 63) were ublished, strong additional evidence has been accumulated to indiate that *C. c. sucklii* after its introduction and rapid spread in the olorado River system has hybridized with the native suckers in very igh frequency. If plans mature, this evidence will be presented by ubbs and Miller, along with data which suggest that the introduction of an exotic species is a main cause of the very high frequency of hybridization between *Catostomus* species and *Pantosteus santa-anae* (Hubbs, Hubbs, and Johnson, 1943 : 47–48, 63) and between *Gila orcuttii* and *Siphateles mohavensis* (Hubbs and Miller, 1943). That the natural derangements caused by the introduction of an exotic are often responsible for a partial breakdown of species lines is a conclusion repeatedly stressed by Huxley (1943).

EVIDENCE FOR HYBRIDIZATION

The interpretation of six specimens as natural hybrids between *Catostomus latipinnis discobolus* and *Pantosteus delphinus delphinus* is based on such criteria as those outlined by Hubbs, Hubbs, and Johnson (1943 : 11–14). Again we have only circumstantial evidence, but to us it seems quite satisfactory.

Both sets of three hybrids were collected with the putative parents. In Beaver Creek no other species of sucker was present, nor was any other expected. In Gunnison River a third species, *Catostomus commersonnii sucklii*, did occur, but the *C. l. discobolus* × *P. d. delphinus* hybrids exhibited none of the particularly diagnostic characters of *C. c. sucklii*, and they were obviously different in the expected features from the hybrids between *C. c. sucklii* and *Pantosteus d. delphinus*.

The conclusions that the breeding seasons of *C. l. discobolus* and *P. d. delphinus* coincide or broadly overlap and that the hybrids stem from spawning at about the time when the parental forms breed are verified by the size of the young in the Gunnison River collection of October 20. The 256 young of the year of *C. l. discobolus* ranged in standard length from 24 to 45 mm. (the two specimens, 77 and 78 mm. long, were interpreted as yearlings). The 841 young of the *Pantosteus* ranged in length from 20 to 53.5 mm. (the 53.5 mm. fish, nearly 10 mm. longer than the next largest, may well have been a yearling). The three hybrids were of similar size: 25, 40, and 43 mm.

The characters of the hybrids are not those of any known or expected species of sucker, but appear to be normal. In several respects they fail to fit either the generic or the specific system. The distinctions that separate *Catostomus* and *Pantosteus* consistently throughout the Colorado River and other stream systems of the Pacific drainage break down in these supposed hybrids.

Like most interspecific hybrids in the fish group, the six specimens hand exhibit a highly distinctive intermediacy between the par- ular parental forms that are presumed to have miscegenated. As is licated in the following section, the intermediacy of the hybrids ns through the whole gamut of characters. On the average the fin ys are intermediate in number. Differences in scale numbers were t determined, for the counts are not greatly different in the parental rms, but the hybrids appear to fall between the two species in the ferential size of the scales fore and aft. Interjacency is also shown the very distinctive lip and mouth structures and in the degree of estinal coiling. Most proportional measurements of the hybrids between those of the parental species. In the young, which are s strikingly different than the adults in lip structure and propor- ns and in which the determination of these characters is more ficult and more subject to error, another set of differences, those of melanophore pigmentation, comes into use. The pigmentary aracters were studied in every one of the several hundred young kers in the collections containing the hybrids here treated. In se respects, too, the hybrids are nicely intermediate.

INTERMEDIACY OF THE HYBRIDS

The yearling hybrids from Beaver Creek were readily recognized such on sorting the collection in the laboratory and would have n identified in the field had the collecting been less hurried, because y differed markedly from each parental species yet strongly re- nbled both. Their intermediacy is very striking. This is par- ılarly true of the trenchant generic characters of mouth structure ubbs, Hubbs, and Johnson, 1943 : 33–36). The upper lip overhangs re than in the *Catostomus*, less than in the *Pantosteus*, and is inter- diate in papillation. Between the lips at each side of the oral disk re is an emargination, where there is a deeper incision in the *ntosteus* but none in the other parental species. The lower lips are re broadly united on the midline than in the *Catostomus*, but are connected than in the *Pantosteus*. The cartilaginous ridge of the er jaw is broader, more truncate, and more sharply shouldered on side than it is in the *Catostomus*, but is less modified than in the er form. On the average the mouth is broader than in the former cies but narrower than in the *Pantosteus*. The snout is more bous and protruding than in *C. l. discobolus*, but less so than is al in *P. d. delphinus*.

TABLE II

PROPORTIONAL MEASUREMENTS OF *CATOSTOMUS LATIPINNIS DISCOBOLUS*,
HYBRIDS, AND *PANTOSTEUS DELPHINUS DELPHINUS*

The measurements are expressed as thousandths of the standard lengt There are given for each item the range of the proportions (for the hybrids th actual figures) and below this the mean and, for each parental species, the standar error. For the size groups (first sets of rows) the standard error is not compute but the number of specimens (in parenthesis) follows the mean.

	Beaver Creek	Gunnison River	
Size group, mm.			
C. l. discobolus	78–125	39–46	24–27
	100 (10)	41 (24)	26 (12)
Hybrids	80, 104, 105	40, 43	25 (1)
	96 (3)	42 (2)	
P. d. delphinus	71–124	37–44	24–26
	90 (14)	39 (22)	24 (13)
Caudal peduncle depth			
C. l. discobolus	65–76	56–79	60–71
	70.8 ± 1.0	69.0 ± 0.9	66.1 ± 0.8
Hybrids	73, 77, 82	69, 70	66
	77.3	69.5	
P. d. delphinus	72–85	67–78	63–75
	79.2 ± 1.1	72.7 ± 0.6	69.4 ± 1.0
Head length			
C. l. discobolus	260–280	262–289	270–297
	270.8 ± 2.4	273.8 ± 1.6	280.3 ± 2.
Hybrids	249, 254, 259	267, 273	264
	254.0	270.0	
P. d. delphinus	234–257	238–264	253–282
	246.0 ± 1.9	250.7 ± 1.4	266.2 ± 2.
Head depth			
C. l. discobolus	163–183	139–184	166–186
	171.3 ± 2.1	172.1 ± 2.0	175.6 ± 1.
Hybrids	167, 169, 170	164, 167	162
	168.7	165.5	
P. d. delphinus	145–168	154–174	162–181
	157.3 ± 1.8	161.7 ± 1.1	170.6 ± 1.
Snout projection			
C. l. discobolus	− 8.0– + 5.5	2.5–13.8	2.2–13.8
	− 3.4 ± 1.6	6.1 ± 0.6	6.7 ± 0.9
Hybrids	8.2, 11.6, 11.6	18.7, 19.7	13.8
	10.5	19.2	
P. d. delphinus	10.6–19.2	14.1–26.1	11.1–24.0
	15.3 ± 0.7	20.1 ± 0.9	19.1 ± 1.1

TABLE II (*continued*)

	Beaver Creek	Gunnison River	
Isthmus width (A)			
C. l. discobolus	44–77	55–88	46–74
	61.9 ± 2.6	66.1 ± 1.5	56.5 ± 2.2
Hybrids	71, 72, 83	71, 82	71
	75.3	76.5	
P. d. delphinus	92–114	61–102	64–85
	102.1 ± 2.1	85.6 ± 2.2	74.2 ± 1.7
Mouth width (B)			
C. l. discobolus	90–110	65–91	65–83
	98.3 ± 1.8	80.0 ± 1.3	73.7 ± 1.5
Hybrids	95, 115, 121	80, 86	79
	110.3	83.0	
P. d. delphinus	108–131	90–107	77–88
	119.7 ± 1.7	98.0 ± 1.0	82.9 ± 1.1
Cartilaginous ridge width (C)			
C. l. discobolus	29–38	24–45	25–45
	35.5 ± 0.8	35.6 ± 1.1	32.6 ± 1.5
Hybrids	50, 53, 53	46, 51	37
	52.0	48.5	
P. d. delphinus	66–75	53–65	30–61
	70.1 ± 0.7	59.0 ± 0.8	50.5 ± 2.2
Lower lip union (D)			
C. l. discobolus	13–17	12–21	10–19
	15.6 ± 0.3	16.5 ± 0.5	13.0 ± 0.7
Hybrids	23, 24, 28	18, 19	14
	25.0	18.5	
P. d. delphinus	33–42	16–40	11–25
	38.1 ± 0.9	23.9 ± 1.2	19.0 ± 1.2
Character index (A + B + C + D)			
C. l. discobolus	190–233	164–225	154–208
	211.3 ± 4.0	198.2 ± 3.1	175.8 ± 4.5
Hybrids	240, 267, 281	221, 231	201
	262.7	226.0	
P. d. delphinus	312–360	235–301	192–250
	330.0 ± 3.8	266.4 ± 3.6	226.7 ± 4.8
Dorsal fin base			
C. l. discobolus	161–190	166–202	154–176
	179.1 ± 3.2	178.3 ± 1.8	164.9 ± 1.8
Hybrids	175, 177, 187	166, 169	142
	179.7	167.5	
P. d. delphinus	128–160	118–160	116–153
	143.2 ± 2.1	137.6 ± 2.4	137.9 ± 3.2

TABLE II (*concluded*)

	Beaver Creek	Gunnison River	
Dorsal height			
C. l. discobolus	203–248	208–249	216–247
	230.9 ± 4.2	230.3 ± 2.2	226.2 ± 2
Hybrids	225, 226, 235	226, 235	208
	228.7	230.5	
P. d. delphinus	188–225	193–232	185–237
	207.1 ± 2.8	210.6 ± 2.2	214.0 ± 3
Pectoral length			
C. l. discobolus	172–211	178–221	170–192
	193.7 ± 3.7	193.1 ± 2.2	178.5 ± 1
Hybrids	205, 206, 209	199, 213	199
	206.7	206.0	
P. d. delphinus	191–217	190–220	180–215
	202.8 ± 2.2	205.7 ± 1.9	193.1 ± 2
Caudal length			
C. l. discobolus	256–298	274–317	264–298
	282.6 ± 4.4	292.1 ± 2.6	280.5 ± 4
Hybrids	252, 276, 276	282 (1)	265
	268.0		
P. d. delphinus	216–278	236–290	253–286
	250.4 ± 5.0	261.4 ± 3.4	268.1 ± 3

The intermediacy of the three yearling hybrids is further indicate by an analysis of the proportional measurements, which were take of the parts that differ in relative size in the parental species (Table I and upper frames of Figs. 1–2). On the average the caudal peduncl is deeper than in the *Catostomus*, slenderer than in the *Pantosteu* and the head is shorter and slenderer than in the former species, but longer and deeper than in the latter. The snout projection is cor sistently greater than in the *Catostomus* specimens measured but less than in most of the *Pantosteus* examples. The isthmus is wide than usual in the *Catostomus*, consistently narrower than in the othe species. The mouth width averages intermediate; the cartilaginou ridge width is consistently interjacent, as is also the length of th union of the lower lips. Uniform intermediacy is also shown by th character index that summates the mouth and isthmus measurements.

The fins as a rule are unexpectedly large. A similar situation ha been noted and attributed to hybrid vigor in certain other hybrids, for example, in *Gila orcuttii* × *Siphateles mohavensis* (Hubbs and Miller, 1943 : 367, 370–374).

In identifying the young hybrids less reliance could be placed on the characters, outlined above, that proved useful in recognizing the yearling hybrids and in indicating them as intermediate between the parental species. In the specimens about 40 mm. long the distinctions used in the half-grown hybrids are still rather readily apparent, but in the young approximately 25 mm. long these differences are too small and too overlapping (Table II and lowest frames of Figs. 1–2) to make possible either a fully trustworthy identification of the hybrids or a completely satisfactory test of their intermediacy. Certain of the characters, however, are reasonably reliable. Thus one can see that the mouth is protractile almost straight downward in the *Catostomus*, but downward and backward in the *Pantosteus*. Furthermore, the greater size disparity of the scales on the anterior and on the posterior parts of the body in the *Pantosteus* is early apparent. In these important respects the young hybrids are intermediate.

As the characters that distinguish the half-grown and adult hybrids from both parental species become decreasingly serviceable in fish grading downward in standard length from about 40 to 25 mm., certain pigmentary differences that gradually fade out at lengths much greater than 40 mm. become very useful in the identification of the hybrids and in the testing of the theory that the characters of the hybrids are intermediate between those of the parental species. The three young hybrids show a weak to moderate development of each of the pigmentary characters, whether the development or specialization of the melanophores in a certain area or manner be diagnostic of the *Catostomus* or of the *Pantosteus*. Thus in all these respects the hybrids again are intermediate.

The more striking of the observed pigmentary differences between the 25– to 40–mm. young of *Catostomus latipinnis discobolus* and *Pantosteus delphinus delphinus* are as follows:

Pigment on side of muzzle. — In *C. l. discobolus* the dark blotch on the side of the snout is abruptly down-curved, because most of the melanophores that lie on the posterior part of the maxillary (showing through the preorbital) are ventral to the superficial dark band that extends horizontally along the side of the head. In *P. d. delphinus* the pigmented area is not abruptly curved, except when the mouth is pulled open, for when the jaws are in normal position the melanophores on the posterior part of the maxillary are covered by the dark band.

Melanophores on ridge underlying nostril. — These color cells are usua small in the *Catostomus*, whereas in the *Pantosteus* they are usually rather marke enlarged.

Black peritoneum as seen through the translucent body wall. — In *C. l. discobo* the black area is less conspicuous than it is in *P. d. delphinus*, because it is m hidden by silvery (guanine) pigment and because it extends up not more tl half instead of distinctly more than half the side of the trunk.

Intestinal canal as seen by the impressions visible through the thin belly wall. The coils are more loosely, less extensively, and less transversely coiled in t *Catostomus* than in the other species.

Pigment on back before dorsal fin. — In *C. l. discobolus* isolated giant mela phores are more conspicuous than the crosswise mottlings and reticulatio which are composed of much smaller melanophores. In *P. d. delphinus* the verse is true. Along the median predorsal line the large melanophores typica form a definite single file in the *Catostomus*, but in the *Pantosteus* are usually t few and too scattered to form such a file.

Superficial melanophores along middle one third of body. — In *C. l. discobo* these cells are relatively small and sparse and over the caudal base are scarc developed, whereas in the other parental species they are larger and thicker a are commonly developed in the skin over the caudal base. In some of the *Pa tosteus* specimens the superficial melanophores (not to be confused with the de lying pigment) are somewhat enlarged and concentrated in the hypural regi but never form a definite basicaudal spot as they do in *Catostomus commerson sucklii* and, less boldly, in the young *C. c. sucklii* × *P. d. delphinus* hybrids.

Deep-lying pigment in the myocommata, forming V's with points on the ax septum. — These marks are usually more prominent in *C. l. discobolus* than tl are in the *Pantosteus.*

Black streak in axial septum on caudal region of body. — In the young of t *Catostomus,* this streak is usually continuous or subcontinuous, rarely disrupt into dashes, and very seldom obsolescent in fish shorter than 40 mm. In t *Pantosteus* the mark is lacking or is represented by slight wisps of pigment.

Deep-lying pigment at base of lower procurrent caudal rays. — Most young *C. l. discobolus* are conspicuously pigmented about these rudimentary ra whereas in nearly all young of *P. d. delphinus* the pigment here is faint or lacki

Deep-lying pigment on hypural plate as seen by transmitted light. — In t *Catostomus* the hypural pigment typically forms two to four dark streaks, tending upward and backward, sufficiently separated so as not to give the appe ance of a solidly filled semicircle. In the other parental species the oblique strea are broader and more diffuse and are conjoined around the posterior edge of t hypural. As a result, the hypural pigment in this species gives the impress of a solidly dark semicircle.

It is highly probable that pigmentary differences, as is oft true, will be found to distinguish the species at even earlier stag Adequate material to test this probability, however, is not at har There is available one series (U.M.M.Z., No. 92248) of 570 specime grading from postlarvae 11 mm. in standard length to early juveni

2 mm. long, but the entire set seems to represent *C. l. discobolus* nd is so recorded in Table I). This collection was made in Green iver near Green River, Wyoming, by Leonard P. Schultz and Allan . DeLacy on June 23, 1931. The largest specimens (22 mm.) and me nearly as large (18 to 21 mm.) agree with the preceding charac- rization of the young of this form of *Catostomus.* Most of those 5 to 21 mm. long differ in some respects. They show the strong axial reak of this sucker. A middorsal row of large melanophores extends om the head to a wedge of smaller specks just before the dorsal fin. here is a dorsal dark band of moderate width, in which the melano- ores in an irregular to even file, toward the outer edge of either side, tending from near the head to the side of the dorsal fin, approach ose of the median predorsal line in size. A black streak marks the se of the procurrent caudal rays, above and below. A fine line tends along and before each side of the anal base and another, ubled in some, continues along the lower edge of the caudal duncle. A few dots usually occur on the middle of the breast and few may accompany the preanal fin fold. There is a dark streak, ten hidden, on the pleural peritoneum. Three blackened areas, creasing in the area forward, are seen on the top of the head. The per part of the opercle bears black specks, as does the muzzle wn to the upper lip. A black streak marks a portion of the lower sterior edge of the orbit. Otherwise the 16- to 21-mm. young are most wholly devoid of pigment. In the series grading from 16-mm. ung to 11-mm. postlarvae several changes (the reverse of the velopment sequence) are observed: the axial streak becomes dotted d undeveloped forward; the predorsal line becomes more of a reak and is usually less extended toward the dorsal fin; the smaller ecks of the dorsal band are not developed; as a result a double file dots stands out, from near the head to the dusky wedge in front the caudal fin; the three blotches on the top of the head become ore discrete and the melanophores of the successive blotches be- me smaller forward; the specks on the opercle and muzzle, the reak on the lower border of the orbit and the peritoneal pigment e little or not at all developed. The entire lot seems to comprise graded series of the single form, but there is no final proof that the *antosteus delphinus* pigment pattern does not grade into the same pression. If the two species should prove alike in the postlarval d very early juvenile stage, the relative numbers of the parental

species recorded in Table I would be in error, overweighed on tl *Catostomus* side. The error would not be large, however, for most the specimens in this big series (certainly all of the larger ones) a definitely referable to *C. l. discobolus.*

In their proportional measurements the young hybrids show mo overlap on the parental species than do the yearlings (Table II ai Figs. 1–2). This is due not only to the fact that the differences b tween the parents are actually less wide and less sharp, but also the circumstance that the measurements cannot be made with pı cision on the very small fish, even though they be taken very careful under a binocular microscope with precision dial calipers. Furthe more, the young appear to be more variable, as though their cha acters were less definitely fixed along the patterns of the respecti species. Despite these circumstances, the measurements of t young, particularly the more critical mouth and isthmus proportio appear to be essentially intermediate. The 25-mm. specimen especially variable in its characters; for instance, the head is smal than usual in *Pantosteus*. Were it not for the confirmation of t pigmentary characters it would have been hazardous to identify tl specimen as a hybrid.

Both lots of hybrids, yearlings as well as young, exhibit an int mediacy in fin-ray counts (Table III) that confirms the interpretati of them as the products of interspecific crossing. The dorsal and t pelvic counts of the hybrids overlap the counts for both paren species, but this would be expected, since the counts for the spec are not invariably different. The overlap between the counts for t parental kinds is eliminated for the Beaver Creek series and is alm circumvented for the Gunnison River series by the use of a sim character index, namely, the sum of the counts for the dorsal and both pelvic fins. In this summary index the intermediacy of the h brids is particularly well demonstrated for the young from Gunnis River, but is not so well indicated for the Beaver Creek yearlin However, the identification of the larger fish as hybrids is especia free from doubt.

Hybrid indices (Table IV) confirm and specify the intermedia of the hybrids. The grand-average index for the counts is 35, in cating a closer agreement with the *Catostomus* than with the *P tosteus*. For the critical measurements of the mouth and isthmus average index of 43 shows a closer approach toward exact interm

TABLE III

Fin Ray Counts of *Catostomus latipinnis discobolus*, Hybrids, and *Pantosteus delphinus delphinus*

	Beaver Creek			Gunnison River		
	Catostomus	Hybrids	*Pantosteus*	*Catostomus*	Hybrids	*Pantosteus*
Dorsal rays						
10	.....	.....	20	.....	.....	22
11	3	1	3	3	2	27
12	12	2	.....	23	.....	1
13	1	.....	.....	23	1	.....
14	.....	.....	.....	1	.....	.....
N	16	3	23	50	3	50
M	11.87	11.67	10.13	12.44	11.67	10.58
SD	0.50	.....	0.34	0.64	.....	0.53
SE	0.13	.....	0.07	0.09	.....	0.07
Pelvic rays *						
8	.....	.....	3	.....	.....	1
9	.....	1	43	.....	1	83
10	26	5	.....	67	5	16
11	6	.....	.....	33	.....	.....
N	32	6	46	100	6	100
M	10.19	9.83	8.93	10.33	9.83	9.15
SD	0.40	.....	0.25	0.47	.....	0.38
SE	0.08	.....	0.05	0.06	.....	0.04
Total dorsal and pelvic rays						
26	.....	.....	1	.....	.....	.....
27	.....	.....	1	.....	.....	.....
28	.....	.....	18	.....	.....	20
29	.....	.....	3	.....	.....	19
30	.....	.....	.....	.....	1	8
31	3	2	.....	1	1	3
32	9	1	.....	17	.....	.....
33	2	.....	.....	16	1	.....
34	2	.....	.....	8	.....	.....
35	.....	.....	.....	8	.....	.....
N	16	3	23	50	3	50
M	32.19	31.33	28.00	33.10	31.33	28.88
SD	0.91	.....	0.60	1.10	.....	0.89
SE	0.23	.....	0.13	0.16	.....	0.12

* The pelvic rays were counted on both sides; hence the number of cases is twice the number of specimens. In computing the standard error of the mean, allowance was made for correlation between the rays in the left and right fins, according to a method to be proposed later (Hubbs and Hubbs, MS).

acy. A still closer approach to the exactly intermediate index of 5 is exhibited by the average of 52 for all proportional measurements The grand average for all counts and all measurements, with eac determination given equal weight, happens to fall at 50. In the tota ensemble of their characters, therefore, the six hybrids may be sai to fall just halfway between the parental species. In the separat characters, however, there is considerable deviation from the perfec index of 50. The value for the fin rays is low, as already indicated For size, however, the index for the dorsal fin is seen to approach tha of the *Catostomus*, whereas the value for the pectoral fin exceeds tha for the *Pantosteus;* in each case the reason is the large size of the fin in the hybrids.

The average index for all characters as calculated for each individual ranges from 33 to 78 for all six specimens and deviates mor than 11 per cent from 50 in only two individuals. For all character counts also included, the average indices for the individuals rang from 28 to 81 (from 34 to 51 in 4 specimens). The most extrem values are for young specimens, which furnish rather unreliabl measurements.

For the yearling specimens, for which fluctuations in the hybri index are caused by normal variations more than by errors in measurement, the average individual hybrid indices for all measurements ma be compared with corresponding figures for the parental species:

Catostomus l. discobolus (10): −31 to 10.5;
Hybrids: 39, 53, and 61;
Pantosteus d. delphinus (14): 74 to 125.

SUMMARY

Hybridization in nature between species of catostomid fishes i confirmed by an analysis of six specimens recently collected i Colorado. They represent a species combination, *Catostomus lat pinnis* × *Pantosteus delphinus*, that was previously known from single very young specimen, and they establish a new subspeci cross, *C. l. discobolus* × *P. d. delphinus*. These forms appear hybridize less frequently than do some other pairs of species in t family. The association of a rare and an abundant species and t crowding of fish on limited spawning grounds appear to explain f one locality why the hybrids at hand were produced, and simil factors may have operated at the other place. A higher rate

TABLE IV

Hybrid Indices for All Characters Studied in *Catostomus latipinnis discobolus*, Hybrids, and *Pantosteus delphinus delphinus*

An index of 50 indicates exact intermediacy, on a percentage scale in which the average for the *Catostomus* is set at, 0 that for the *Pantosteus* at 100. One unreliable index, for a character in which the parental forms differ by less than 4 per cent, is enclosed in parentheses and is disregarded in computing the averages for individual hybrids and for characters. The two summary character indices are also eliminated in computing the averages.

	Beaver Creek specimens				Gunnison River specimens				Grand Average
	80 mm.	104 mm.	105 mm.	Average, 80–105 mm.	40 mm.	43 mm.	Average, 40–43 mm.	25 mm.	
Dorsal rays (A)	– 7	50	– 7	12	– 30	77	23	77	27
Rays, both pelvics (B)	15	15	55	28	28	28	28	113	42
Index (A + B)	5	26	26	19	2	50	26	97	34
Average, ray counts	4	32.5	24	20	– 1	53	26	95	35
Caudal peduncle depth	74	26	133	78	0	27	13	– 3	43
Head length	48	68	88	68	3	29	16	116	59
Head depth	31	9	16	19	49	78	63	(272)	37
Snout projection	80	80	61	74	90	97	93	57	77
Isthmus width (C)	25	23	52	33	26	82	54	82	48
Mouth width (D)	– 15	78	106	56	0	33	17	58	43
Cartilaginous ridge width (E)	42	51	51	48	66	44	55	25	47
Lower lip union (F)	33	55	37	42	34	20	27	17	33
Index (C + D + E + F)	24	47	59	43	33	48	41	50	43
Dorsal fin base	6	11	– 22	– 1	23	30	27	85	22
Dorsal height	– 17	21	25	10	21	– 23	– 1	149	29
Pectoral length	135	124	168	142	46	157	101	146	129
Caudal length	20	95	20	45	.....	32	32	125	58
Average, measurements	39	53	61	51	33	51	42	78	52
Grand average	34	50	50	46	28	51	40	81	50

crossing results when an exotic species becomes associated with
native form.

A variety of circumstantial but seemingly reliable evidence supports the interpretation of these specimens as interspecific hybrids.

The hybrids are intermediate between the parental species i
almost all their characters. This is perhaps most strikingly true o
the trenchant generic differences in mouth structures, but applie
also to the projection of the snout, the width of the isthmus, an
various other head and body proportions. The fins, however, ar
unexpectedly large. The characters that show intermediacy in th
larger fish become less serviceable in the smaller young, though suc
characters as the direction of protractility of the mouth and th
disparity in the size of the scales anteriorly and posteriorly are earl
apparent, and are intermediate in the hybrids. A study of numerou
pigmentary differences, most of which disappear with age, verifies th
identification of the young and the determination of their character
as intermediate.

Scripps Institution of Oceanography
University of California
La Jolla, California

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Seaweed Resources of North America and Their Utilization[1]

From the coasts of Nova Scotia, Maine, Massachusetts, North Carolina, California and Lower California, seaweeds are harvested that yield agar, algin, carrageenin and iridophycin for industrial use.

C. K. TSENG
Scripps Institution of Oceanography, La Jolla, California

Introduction

FOR ages, before the advent of white men, the American Indians on the Pacific Coast gathered seaweed for food, and since the latter part of the last century, the Chinese residents in California have also regularly harvested them for the same purpose. On the Massachusetts coast, the collecting of Irish moss has been an established industry for over a century, and for many years East Coast dulse has been sporadically on sale in the markets of Boston, Philadelphia and New York. Utilization of the seaweed resources of North America, therefore, is not a wholly recent matter, but until lately the harvesting and utilization of these marine plants in America were of a rather primitive and sporadic nature. No concerted effort was made to exploit them on an industrial scale, and it took one World War after another to place American seaweed industries on a firm industrial footing. These industries and the natural supplies of seaweeds upon which they are founded, as well as the utilization of those resources, are discussed in this article.

America's Seaweed Industries

Potash, Acetone, Kelpchar, Iodine. Shortly before and during World War I there was a serious shortage of potash in the United States, since the supply of this chemical, so vitally important in modern scientific agriculture, at that time came entirely from Germany. Several domestic sources of potash were soon developed, however, through the concerted efforts of the United States Government and of private industry. One of these sources was the California seaweed known as the "giant kelp" (*Macrocystis pyrifera* (Turn.) Ag.). For the duration of World War I, this kelp remained second only to natural brines as a source of American potash. Through a unique fermentation process, acetone and calcium acetate for the manufacture of smokeless powder were also derived from *Macrocystis*. Two other valuable chemical products, iodine and a bleaching carbon known as "kelpchar", were also obtained.

The Pacific kelp industry thus prospered for a few years, with as many as ten factories engaged in the production of potash, acetone, kelpchar and iodine from the California giant kelp. The kelp factory of the Hercules Powder

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Company alone handled as much as 24,000 tons of fresh kelp per month. Mechanical harvesters were devised for cutting the kelp, and production of potash and other chemicals was a feat of modern chemical engineering. Thus, under the stimulus of war, utilization of kelp became well established as a modern industry within two or three years. This potash-from-kelp industry was, however, short-lived, and immediately upon cessation of hostilities, all the kelp factories suspended operation. Since then the American potash-from-kelp industry has not been revived; most probably it will never return, since potash, iodine and acetone can now be obtained more cheaply from sources other than seaweeds.

Algin. The Pacific kelp industry, however, came back in other forms in the late 1930's and is now engaged principally in the production of algin. This is a valuable colloidal substance occurring in many brown algae, especially kelps, and is extensively employed in modern food and other industries in America. In recent years the common Atlantic kelps, *Laminaria digitata* Lamour (horsetail kelp) and *L. saccharina* (L.) Lamour (broadleaf kelp), have also been utilized in the manufacture of algin, and today the annual production of algin in America is estimated at two to three million pounds.

Agar. In the recent war there was no longer a shortage of potash or acetone. There was, however, a shortage of another important material, agar, which is vitally needed in public health work. Agar is derived from red seaweeds, chiefly from members of the genus *Gelidium.* Most of it came from Japan prior to the outbreak of war in the Pacific. Although it has been manufactured in the United States since 1919, domestic agar production amounted to only a small percentage of the total American consumption. Until the outbreak of the war, America's agar industry was not successful, principally because of keen Japanese competition an of the high cost of production. The industry greatly expanded, however, during World War II, and there were fiv factories engaged in producing this vita product during the war. Production a its peak reached 165,954 pounds in on year. At present, however, only thre concerns are still active in processin agar. The seaweeds used are agarweed *Gelidium cartilagineum* (L.) Gaill. fro California and Baja California, Mexico on the Pacific Coast, and *Gracilaria confervoides* (L.) Grev. from Beaufort North Carolina, on the Atlantic. Othe species of *Gelidium, e.g., G. arborescen* Gard. and *G. nudifrons* Gard., are employed indiscriminately with the agarweed in agar manufacture. On th Atlantic Coast *Gracilaria foliifer* (Forssk.) Borgs. is similarly used.

Carrageenin. Although the Iris moss industry may claim to be the oldes seaweed industry in America, it is onl in recent years that it has been established as a modern industry. Formerl the industry amounted mainly to harvesting and preparing the seawee *Chondrus crispus* (L.) Stackh. and selling it as a crudely cured and partiall bleached ''moss''. The buyer had to extract the colloid carrageenin by boilin the seaweed in water and straining th solution through cheese cloth. In th late 1930's the industry started to produce carrageenin in the form of a purified dry powder, but production in larg quantities was not achieved until the las few years. At present at least four firm are engaged in producing this produc and about half a million pounds wer prepared in 1945. The 1946 productio was expected to reach 800,000 pounds The ''moss'' is collected and cure mainly in Massachusetts, Maine and th Canadian Maritime Provinces, and th dried black or bleached ''moss'' is sen to Scituate, Mass., Passaic, N. J., or Chicago, Ill., for the extraction and preparation of carrageenin.

Iridophycin. Production of the seaweed colloids or phycocolloids—algin, agar, carrageenin—constitute the three principal seaweed industries in America. Since 1945 one firm has been engaged in the production of a fourth phycocolloid, iridophycin, from *Iridophycus flaccidum* Setch. & Gard. and *I. splendens* Setch & Gard. which are harvested from the California and Oregon coasts. The most important non-colloid product is kelp meal which is either made into kelp tablets for human consumption or mixed with alfalfa and other substances into animal feeds. The California giant kelp, *Macrocystis pyrifera,* and the bladder kelp, *Nereocystis Luetkeana* (Mert.) Post. & Rupr., are both used for this purpose.

Food. During World War II, the leafy parts of the bladder kelp were harvested and dried to serve for food among Oriental residents, especially the Japanese in relocation centers, as a substitute for the Japanese kombu, *Laminaria japonica* Aresch., then unavailable because of the war. Both laver and dulse are still being harvested for human consumption.

Figure 1 is a systematic arrangement of the useful American seaweeds and their products in recent years.

America's Seaweed Resources

America's resources of useful seaweeds may be grouped, as indicated in the accompanying diagram, into kelps, agarophytes, carrageens, and other red seaweeds.

Kelps. The most valuable seaweed resource in America is undoubtedly the great abundance of kelps. It is not inappropriate, therefore, to remark on the origin and usage of the term "kelp". In the early part of the eighteenth century it was discovered in Scotland, at a time when there was a great demand for soda ash in the manufacture of soap and glass, that if seaweeds were burned their ash

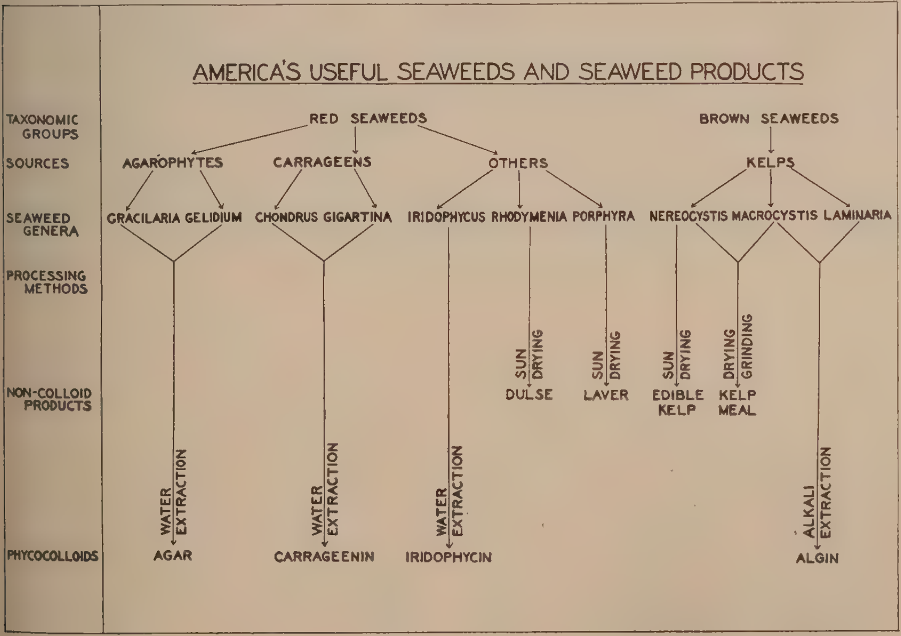
AMERICA'S USEFUL SEAWEEDS AND SEAWEED PRODUCTS
TAXONOMIC GROUPS
SOURCES
SEAWEED GENERA
PROCESSING METHODS
NON-COLLOID PRODUCTS
PHYCOCOLLOIDS
RED SEAWEEDS
BROWN SEAWEEDS
AGAROPHYTES
CARRAGEENS
OTHERS
KELPS
GRACILARIA
GELIDIUM
CHONDRUS
GIGARTINA
IRIDOPHYCUS
RHODYMENIA
PORPHYRA
NEREOCYSTIS
MACROCYSTIS
LAMINARIA
SUN DRYING
SUN DRYING
SUN DRYING
DRYING GRINDING
DULSE
LAVER
EDIBLE KELP
KELP MEAL
WATER EXTRACTION
WATER EXTRACTION
WATER EXTRACTION
ALKALI EXTRACTION
AGAR
CARRAGEENIN
IRIDOPHYCIN
ALGIN

Fig. 1.

was a good source of soda. A seaweed-ash industry was thus born in Scotland and Ireland which was lucrative and important from about 1720 to 1830. To apply to the then valuable seaweed ash, a word of unknown origin, "kelp" was used. In the British Isles the meaning of this word has remained unchanged. The first application of the word to seaweeds themselves, rather than to the ash, appears to have been to an edible New Zealand seaweed called "Bull Kelp" which "has a thick stem, and flat oval-shaped leaf, and is about the thickness of sole-leather". Later this kelp was identified with *Laminaria potatorum* Lamour, a synonym of *Durvillea antarctica* (Cham.) Hariot. When the word "kelp" became known in America in the latter part of the last century, it was applied to certain large brown seaweeds, and *Nereocystis Luetkeana* of the Pacific Coast became "giant kelp", which term was later also applied to *Macrocystis pyrifera* and tw others. Eventually they were merel called "kelp". As it is used amon botanists nowadays, "kelp" refers to al members of the brown algal order Laminariales with large, flat, leaf-like fronds although occasionally one finds the wor loosely and erroneously used in application to seaweeds generally.

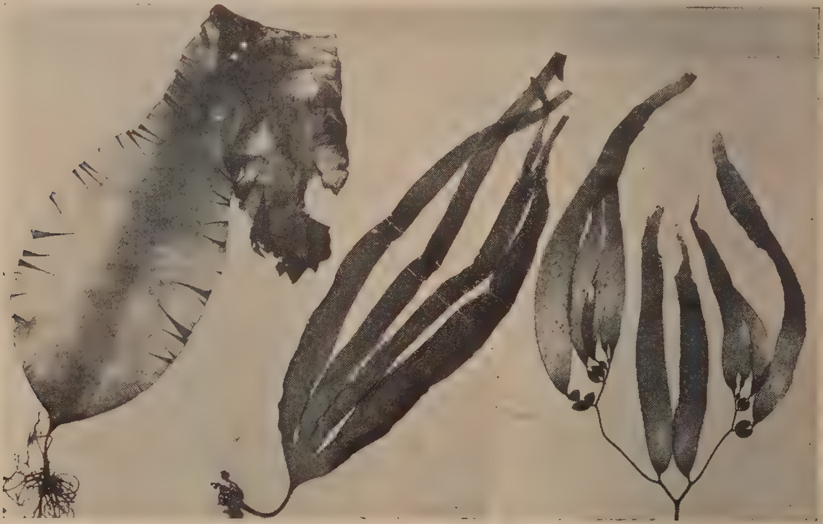

FIG. 2. Three American kelps of commercial importance. The broadleaf kelp (*Laminari saccharina*) and the horsetail kelp (*L. digitata*), at the left and center, are both found along th East Coast, available in commercial quantities north of Cape Cod. At the right is a very young plant of the California giant kelp (*Macrocystis pyrifera*) which forms extensive beds from Cedro Island, Mexico, to Point Conception, California. These three kelps are the American sources o algin, used in a variety of ways described in this article. (*Courtesy of Dr. William Randolp Taylor, of the Scientific Monthly and of the Journal of The New York Botanical Garden.*)

Four species of kelp are utilized i America, two giant kelps on the Pacifi and two smaller kelps on the Atlanti seaboard. Among them the most important is undoubtedly the California gian kelp, *Macrocystis pyrifera.*

Macrocystis. While there are two species of *Macrocystis* on the American Pacific Coast, *M. pyrifera* is the only one commercially utilized in the algin and kelp meal industries, the other species being available only in small quantities The former is a truly "giant" kelp and is undoubtedly the largest seawee known. While it has been reported by earlier authors to attain the enormous length of 1,000 feet, on the American Pacific Coast the largest plant ever actually measured and recorded was about 140 feet long. A perennial plant, it grows on rocky bottoms free from shifting sand, 25 to 90 feet below the water surface. It grows best in places where there is a continuous swell; and where environmental conditions are favorable, it forms extensive beds from a few hundred yards to two or three miles wide and several miles long. From Cedros Island, Baja California, in the south, to Point Conception, California, in the north, it is practically the only constituent of the kelp beds. Northward it is a minor component of the beds along the coast from central California to southeastern Alaska.

This giant kelp attaches itself to rocks by means of a large conical holdfast, composed of long, densely compacted, branched haptera. It has a stipe which is usually four or five times forked near the base. The branches of the stipe bear blades unilaterally at regular intervals. New lateral blades are formed by asymmetrical splitting of the terminal blade from base to apex. Each mature lateral blade has a short stalk, and a subglobose to spindle-shaped basal pneumatocyst or air bladder. The blade is lanceolate, undivided, up to 80 cm. long and 40 cm. broad, and has an irregularly corrugated surface with denticulate margins.

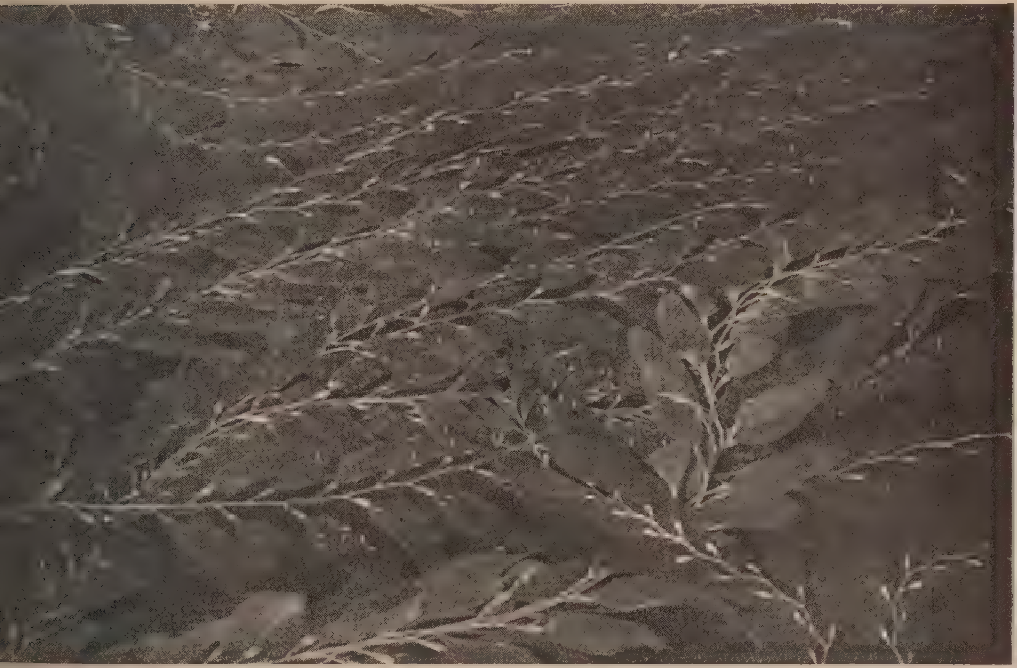

FIG. 3. Fronds of the California giant kelp (*Macrocystis pyrifera*) floating on water near Laguna Beach, Cal. (*Courtesy of the U. S. Fish & Wildlife Service and of the Journal of The New York Botanical Garden.*)

In the early days of the American kelp industry macrocystis was gathered from the beach where it was washed ashore, or whole clumps destructively pulled up by means of a cable and hoist; or the fronds were dragged into a skiff with a hook and cut off with a long knife. All these methods required too much labor and were too inefficient for an American industry to be successful. The mechanical harvester which was later devised solved the labor problem and contributed greatly to the success of the Pacific kelp industry.

A mechanical kelp harvester is a motor-run barge equipped with a modified mowing machine, having a horizontal cutting blade at a depth of about four feet and an endless chain elevator which hoists the kelp on board. The harvesting machine is placed in the bow, with the blade cutting directly ahead of the boat. The knife is considerably shorter than the beam of the boat, and is generally 10 to 20 feet wide. The elevator is as broad as the swath. Its lower sprocket wheels are immediately back of the cutter bar, and it is driven at rather high speed, so as to pick up the cut kelp before the waves wash it away. A knife at each side of the elevator, and parallel with it, serves as an edging device to cut the kelp clear at the sides. Such a barge can harvest and carry as much as 300 tons in a single load. Harvesting is carried out in calm weather throughout the year. By cutting the beds in rotation, they can be periodically worked; and a sustained yield is assured.

FIG. 4. A kelp harvester of the Hercules Powder Company during World War I. (*Courtesy of the Hercules Powder Company.*)

There are no figures available as to the cost of harvesting the giant kelp, since kelp firms operate their own harvesters and do not purchase help from outside sources. Estimates have been placed between two and five dollars per ton of fresh kelp.

Nereocystis. Of the three other giant kelps, *Nereocystis Luetkeana,* the bladder kelp, also known as the "ribbon kelp", is the only one commercially exploited, although to a much less extent than macrocystis. Although an annual, nereocystis grows to gigantic size within a year plants over 100 feet long being reported and forms extensive beds like those of macrocystis. The plant has a hemispherical holdfast consisting of densely compacted branched haptera, and an elongated, subcylindrical stipe, gradually broadening upward and terminating in a subglobose pneumatocyst, the apex of which bears four short flattened four or five times dichotomous branches. These bear 32 to 64 long linear undivided smooth blades which may be over ten feet long and one foot broad.

It has been reported that mechanical technique was used in cutting the nereocystis in the Puget Sound area during World War I. Utilization of the bladder kelp, however, has never been on a large scale, and it is highly doubtful that mechanical harvesting could be carried out economically on small scale operations. Along the central California coast, a Monterey and other nearby regions, the rather ancient method of reaping the kelp by hand with large scythes from scows has been used.

During World War II, large quantities of this kelp were harvested for food as substitute for the Japanese kombu (*Laminaria japonica*), only the leafy parts of the fronds being utilized. The war-time production was about 100 ton of the dried nereocystis per annum. Being thinner and less tasty than the Japanese kombus, the bladder kelp is con sidered inferior in quality, and its production was terminated shortly after cessation of hostilities in the Pacific. Dried leafy parts of the bladder kelp cost about $400 per ton.

Pacific Kelp Beds. Thanks to the extensive surveys of the kelp beds along the Pacific Coast of North America conducted by the United States Department of Agriculture in the years 1911–1913, we have a fairly good knowledge of their approximate size, location and productivity at that time. The following table summarizes the result of this investigation:

TABLE I

Area and Productivity of Pacific Kelp Beds
(Compiled from data of Cameron, Crandall, Frye and Rigg, 1915)

Region	Area sq. miles	Fresh kelp tons	Constituents of the beds, %				
			Macrocystis	*Mac. + Ner.*	*Nereocystis*	*Ner. + Ala.*	*Alaria*
1. Cedros Island, Mexico, to San Diego, Calif.	91.36	16,979,800	100	......	......	......	......
2. San Diego to Point Conception	97.92	18,195,300	100	......	......	......	......
3. Point Conception to Cape Flattery	36.24	4,377,400	17	7	76	......	......
4. Puget Sound	5.00	520,000	Minor	......	Major	......	......
5. Southeast Alaska	70.78	7,833,000	18	......	78	......	4
6. Southeast Alaska (estimated)	70.78	7,833,000	......	......	......	......	......
7. Western Alaska	17.86	3,567,000	......	......	55	33	12
Total	389.94	59,305,500					

Conception the predominant constituent of kelp beds was *Nereocystis*, with *Macrocystis* and *Alaria* in minor quantities. Survey of the coast along southeastern Alaska was incomplete and covered perhaps less than half of the region. Cameron therefore added an additional estimate to allow for the region not surveyed.

The foregoing 1911–1913 estimate of kelp supplies in the Pacific beds was undoubtedly much too high, for later harvestings yielded less than 10% of the estimated amount. There are plentiful kelps growing in places where, for one reason or another, it is not economically practical to harvest them. Actual cutting of macrocystis in the years 1916–1920, between San Diego and Point Conception, showed the highest annual yield at 394,974 tons in 1917, which amount was slightly over 2% of the estimate.

It is to be noted that this survey included three kinds of giant kelp, namely, *Macrocystis pyrifera*, *Nereocystis Luetkeana* and *Alaria fistulosa* Post. & Rupr. In the first and second regions the kelp beds consisted practically entirely of macrocystis, with some *Pelagophycus porra* (Leman) Setch. the elk kelp, in scattered groups along the outer edge of the beds. *Macrocystis* being a perennial plant, determination of the yield of such beds was based on two cuttings per annum. North of Point

Wohnus in 1942 made a careful survey of the three kelp beds in the region between La Jolla and San Diego, California. He found a considerable decrease in area since the 1911 and 1934 surveys (Table II).

The numbering of the beds is based on the official kelp chart of the California State Fish and Game Commission. According to Wohnus (personal communication), the 1911 figures were obtained by measuring the areas of the kelp beds on the maps prepared by Crandall. The 1934 data were based on the Coast and Geodetic Survey map, in which the outlines of these California coastal kelp beds were indicated. Concerning the general condition of the beds, Wohnus stated that there were definite signs of improvement. Although in some areas, such as beds No. 2 and 3, the plants have not yet regained the extensive growth described in previous surveys, there are a few regions in which kelp is now growing where it had not been reported previously. Wohnus believed that, with care and proper regulation, the supply of kelp can be maintained and the present yield increased.

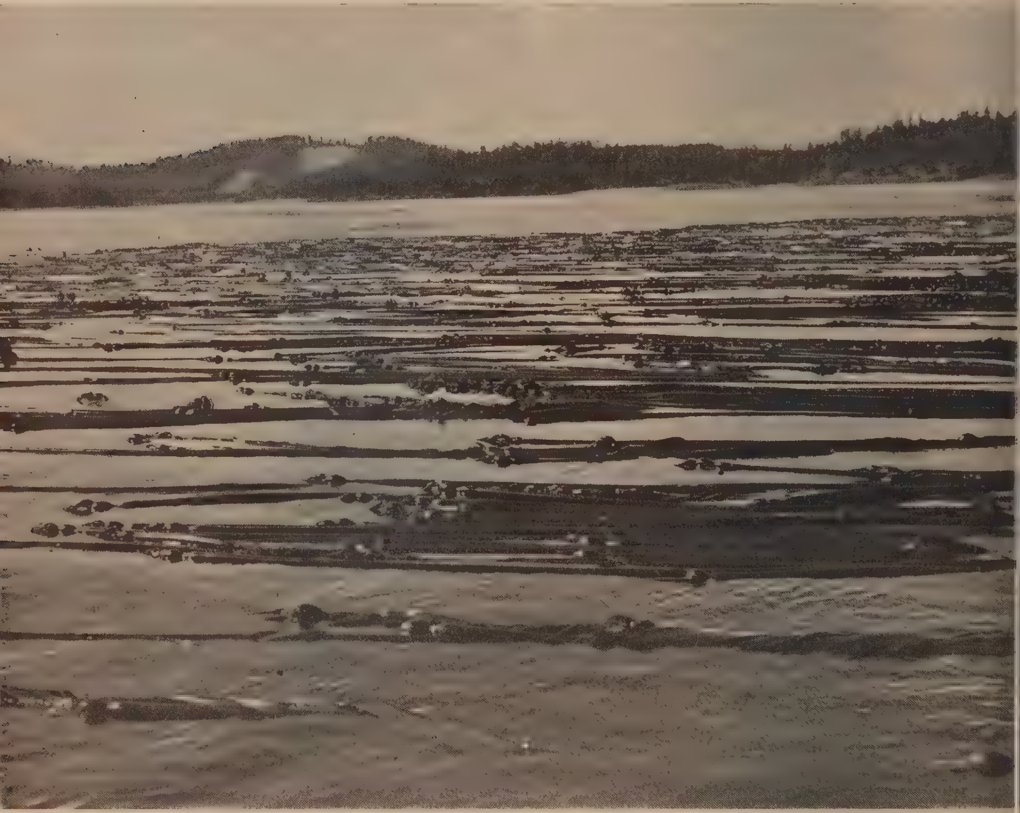

FIG. 5. Fronds of the bull or bladder kelp (*Nereocystis Luetkeana*) floating on the waters of Puget Sound. (*Courtesy of Dr. Robert H. Tschudy and of the Journal of The New York Botanical Garden.*)

Kelp Production in California. Tabulated monthly records of the actual kelp production in California during and immediately after World War I have been published. Large scale harvesting started in August, 1916 and stopped in November, 1918. Commercial cutting of

TABLE II

Changes in Areas in Statute Miles of Three Kelp Beds in the La Jolla–San Diego Region

Bed No.	Year	Area sq. statute miles	Change over 1911		Change over 1934		Remarks
			Actual area change	Per cent of change	Actual area change	Per cent of change	
2	1911	1.4					Heavy
	1934	0.88	–0.52	–37			Scattered
	1941	0.50	–0.90	–66	–0.38	–43	Very thin
3	1911	4.08					Heavy
	1934	2.77	–1.31	–32			....
	1941	2.14	–1.94	–47.5	–0.63	–22.7	Thin
4	1911	2.1					Heavy
	1934	2.6	+0.5	+23.8			....
	1941	2.5	+0.4	+19	–0.1	– 3.8	Medium

the kelp, however, was continued, although on a much smaller scale, for two or three years after the war until all the kelp factories were shut down. The largest annual production was 394,974 tons in 1917.

It should be noted that the production in 1918, namely, 390,863 tons, was only for the period January through October. If kelp was harvested in November and December, proportionally the 1918 production would reach a record high of about 500,000 tons. Since cuttings were made in places more accessible and closer to the operating plants, there were undoubtedly similar quantities of kelps in less accessible places which were not harvested. It is not unreasonable to believe, therefore, that the coastal region between San Diego and Point Conception, with judicial cutting, could produce as much as a million tons per annum, which is slightly more than 5% of the 18,195,300 tons estimated for this region in 1911–1913. On the same basis, the productivity of the Pacific kelp beds may be placed at about three million tons per annum.

TABLE III

Monthly Records of California Kelp Production, 1916–1920, in Tons of Fresh Kelps

Month	1916	1917	1918	1919	1920
January	1,424	37,100	43,118	1,150	2,136
February	3,310	33,733	24,429	930	1,770
March	3,310	29,995	41,916	1,999	1,970
April	3,310	24,249	43,009	2,101	1,508
May	3,310	41,711	45,838	1,771	2,432
June	3,310	41,631	35,022	877	2,136
July	3,310	24,903	42,084	1,380	2,290
August	37,784	25,612	50,507	1,565	1,955
September	19,135	32,739	35,395	587	2,365
October	10,720	35,522	33,780	1,791	1,950
November	17,757	36,582	....	1,184	2,668
December	27,857	31,197	....	1,315	2,284
Total	154,537	394,874	390,863	16,613	25,374

Through the kindness of the California Division of Fish and Game, the writer has obtained monthly records of kelps actually harvested in the last six years by the kelp industry. Cutting of macrocystis is conducted between San Diego and Point Conception. It is to be noted that the present annual kelp harvest averages about 56,000 tons, or only slightly more than one tenth of that during the peak production years, 1917 and 1918.

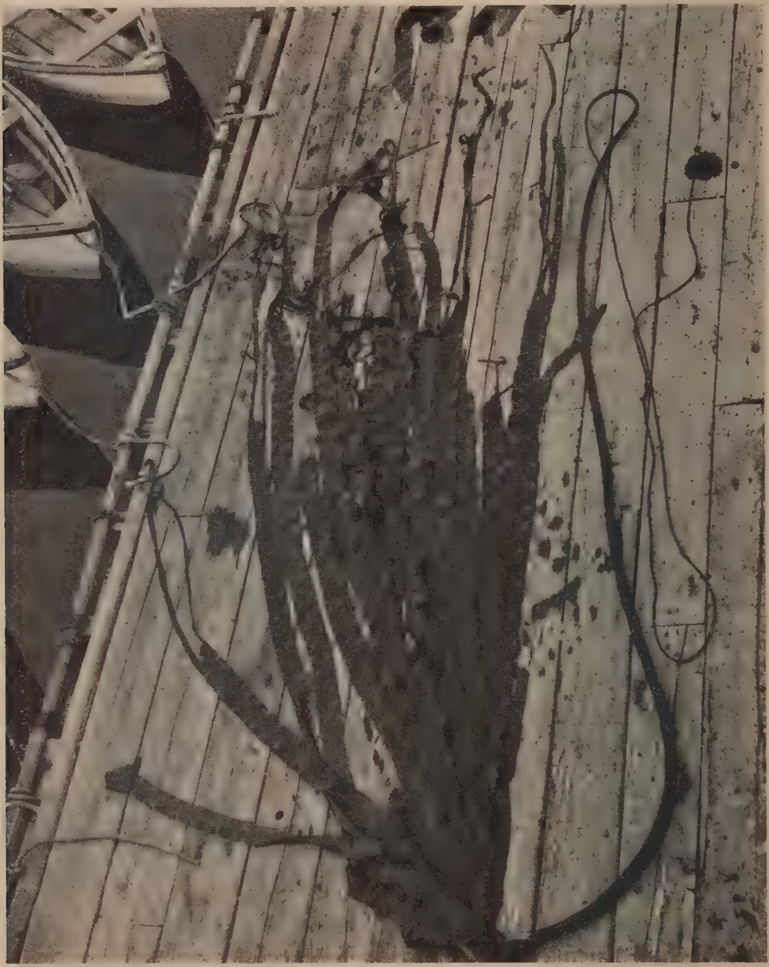

FIG. 6. Bull or bladder kelp (*Nereocystis Luetkeana*). When dried and ground it is use for making kelp pills for humans and kelp meal for livestock rations. (*Courtesy of Dr. Rober H. Tschudy and of the Journal of The New York Botanical Garden.*)

Regulations. In California persons engaged in harvesting kelp or other aquatic plants for commercial purposes are required to have a license whic costs them ten dollars per year. In addition, there is a privilege tax on kelp and other seaweeds at five cents per to of wet weights. One may also lease kel beds, not exceeding 25 square miles in area, for a period of 15 years, upon payment of $40.00 per square mile. Kelps harvested from leased beds are taxed at three cents per ton of wet weights, in addition to the license and leasing fees.

Laminaria. Two species of kelps are utilized on the Atlantic Coast of North America. They are the broadleaf kelp, *Laminaria saccharina,* and the horsetail kelp, *L. digitata.* Both have a firm holdfast, a distinct stipe and a large broad blade, simple in the former and digitately divided in the latter species. The blades are smooth and yellowish to olive brown and may reach ten feet or more n length. They grow on sublittoral rocks, and occur in commercial quantities from Cape Cod northward. Most of the Atlantic kelps used in the algin industry come from the waters off Nova Scotia. Harvesting is effected with a grapple hauled at a depth of 12 to 15 feet from a power boat, and to a lesser extent by hand dragging or sickling from a dory. The harvesting season extends from June to December.

Laminarias do not float on the surface of the water. Kelp beds consisting of them are therefore not as readily surveyed as the giant kelp beds of the Pacific Coast. There are no data as to the supply and harvest of kelps on the Atlantic Coast. We may obtain some idea, however, as to the amount of kelp harvested on the Atlantic Coast, on the basis of actual alginate production, which amounted to about 300,000 pounds in 1944. Since the two laminarias contain on the average about 4% of algin, on the basis of fresh weight, the minimum annual production of fresh kelp should be at least 4,000 tons, or slightly less than 10% of the current Pacific Coast production. There are reasons to believe, however, that the potential kelp resources of the Atlantic Coast are many times the above estimate.

There are several species of *Laminaria* which abound on the Pacific Coast, but to date, none has been utilized. Commercial utilization of laminarias, in general, is handicapped by the necessity of harvesting by manual labor, which increases tremendously the cost of the raw material for the industry. If mechanical means could be devised to gather them economically, there is no doubt that the laminaria resources of America could be more thoroughly exploited.

Agarophytes. The two principal agarophytes in America are *Gelidium*

TABLE IV

MONTHLY RECORDS OF CALIFORNIA KELP PRODUCTION, 1940–1945, IN TONS OF FRESH KELPS

Month	1940	1941	1942	1943	1944	1945
January	1,671	4,417	5,672	3,868	4,256	3,866
February	2,511	2,184	5,967	2,928	2,768	2,990
March	3,231	2,191	6,514	3,683	4,655	3,090
April	3,200	3,281	4,078	4,136	4,519	4,372
May	5,007	4,112	5,506	4,920	5,007	5,340
June	6,283	5,281	5,311	5,846	5,963	6,454
July	6,390	7,274	5,715	5,371	5,410	5,882
August	6,142	5,465	5,726	3,240	5,509	5,005
September	5,426	3,337	5,127	2,323	3,667	5,399
October	7,189	6,733	4,417	3,261	5,393	5,863
November	7,063	5,810	3,814	3,978	4,352	6,584
December	4,897	5,632	4,255	4,414	1,536	4,338
Total	59,010	55,717	62,102	47,968	53,035	59,183

cartilagineum and *Gracilaria confervoides.* The term "agarophyte", originally spelled "agarphyte", was coined by the writer in 1944 to designate red algae utilized in the manufacture of agar, so as to avoid using the term "agar" to apply to both the raw material and the dried extract. Formerly *Gelidium* was the only group used commercially in the American agar industry, but when the discovery of a rich *Gracilaria* resource in the Beaufort, N. C., region was made by Humm in 1942, a new agar industry based on *Gracilaria confervoides* was born on the East Coast.

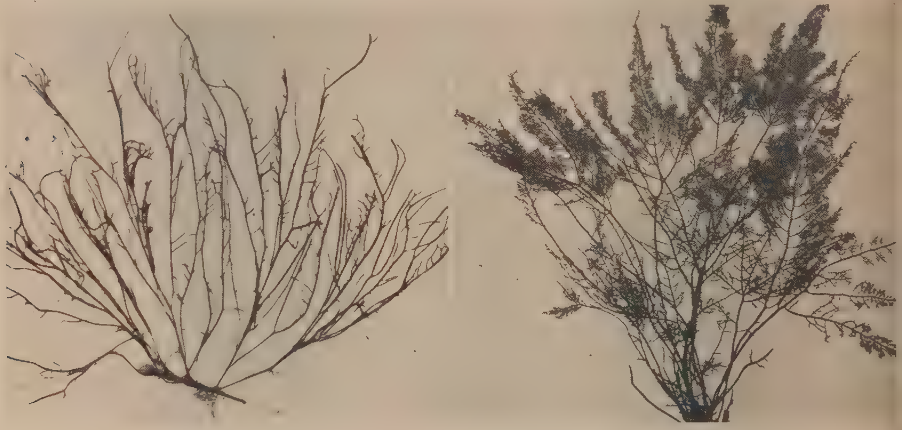

FIG. 7. Principal agarophytes used in the American agar industry, the California agarwee (*Gelidium cartilagineum* var. *robustum*, right) and East Coast agarweed (*Gracilaria confervoides* left). (*Courtesy of U. S. Fish and Wildlife Service and of the Journal of The New York Botanica Garden.*)

Gelidium. The "agarweed" of commerce is the maroon or purplish-red Californian *Gelidium cartilagineum* var. *robustum* Gard. This alga is found in commercially harvestable quantities in southern California and Baja California, Mexico, between Point Conception in the north and Magdalena Bay in the south. Although it grows very well in the Monterey region along the central California coast, its growth there is generally sparse and rarely dense enough to warrant commercial gathering.

This plant has a characteristically naked stipe, sometimes as much as seven cm. in length. It is repeatedly pinnately branched and the young branches are typically geniculate, *i.e.*, the outer ends are almost parallel with branches from which they arise. Later the branches usually opposite but sometimes alternate straighten and stand at about a 45° angle. The entire plant reminds one of the frond of a fern and is hence sometimes known as "sea-fern". It grows in tufts and attaches itself firmly to the rocky substratum by numerous rhizoida filaments. While it has been reporte by professional harvesters to reach height of more than five feet, the larges specimens seen by the writer were abou four feet tall. The plant is generally considered to be harvestable when on and a half to two feet in height.

Gelidium cartilagineum is typically sublittoral plant, growing from the low est spring tide level to a depth of 40 t 50 feet. It does not grow in extensiv beds, as does *Macrocystis pyrifera,* bu is generally found in comparativel small concentrations, localized on th tops or at the edges of rocks or boulders n places where the tidal current is strong. Consequently mechanical harvesters for it have not yet been successfully devised, and harvesting has to be effected by raking or by diving and hand-picking. Raking is, however, rarely employed, and is possible only when the water is extremely calm and rather shalow. Before the war some Japanese harvesters who were experienced in raking seaweeds gathered tons of this agarophyte from the San Pedro breakwater. The majority of harvesters dive and hand-pick the seaweed, and, with a few exceptions, use a complete diving rig.

An agar diving boat is generally a small fishing boat about 30 feet long, equipped with air compressor and heavy rubber hose to supply air for the diver while he is working under water. The crew consists of three persons, a boat operator, a diver and a life-line tender. The last mentioned takes care of the air-ine and the life-line; the latter is a rope with one end tied around the waist of he diver and the other end held tightly by the tender. By signals, as indicated by the number of pulls by the diver on he rope, the line tender knows whether o lift up the harvest or to haul up the diver. While generally there is a single rained diver in a boat, there may be two. In this case they alternate as life-line ender and diver. This system has the advantage of better working efficiency and increases the harvest per diving boat by as much as 50%.

While the general location of commercial quantities of agarweed is known to he divers, they have to hunt for the particular spots where plentiful supplies of he plant are available. Generally speaking, *Gelidium* growths are readily noticeable by experienced divers, because of the presence of the bryozoan *Membranipora* on the older parts of the plants. Experienced agar harvesters have also claimed that wherever one finds the "goldfish" garibaldi (*Hypsypops rubicunda*), one may expect to find good growths of *Gelidium* in the near vicinity.

Since *Gelidium* grows most abundantly around the edges and on the slanting surfaces of rocks and boulders in places where the water is generally turbulent and the water movement fast, the agar diver usually has to crawl from one rock to another, and occasionally grasps the large kelps for support. With one hand he carries a basket made of small ropes; with the other he pulls a bush of the agarophyte from the rocks and puts it into the basket. When he has filled the basket he ties it to his life-line and pulls the rope twice. Upon receiving the signal, the life-line tender hauls up the basketful of agarweed, weighing between 60 and 75 pounds, and lowers an empty one to the diver. When the harvester is tired, he pulls the rope three times, and the vigilant life-line tender quickly pulls him up.

An experienced diver generally works continuously for one to two hours under water. Then he comes up for a short rest. He may dive two or three times a day, working under water for four or five hours. The diving boat usually goes out in the early morning, since the ocean is as a rule quieter in the morning than in the late afternoon. The actual diving hours average about four per day with a single diver and six with two divers on the same boat.

The quantity of agarweed that a diver can gather per trip depends upon his experience, the condition of the sea and the abundance of the *Gelidium* growths. Under the best conditions a diver may pull as much as one and a half tons of fresh agarweed per diving day. For an average diver working under the usual conditions in southern California, however, a harvest of 1,500 pounds of fresh weed per day is considered very satisfactory.

The agarweed thus harvested is spread

on level ground and dried in the sun, but is not washed or bleached, as is done with the Japanese tengusa. In California fresh agarweed is worth about $80, and dry about $350, per ton.

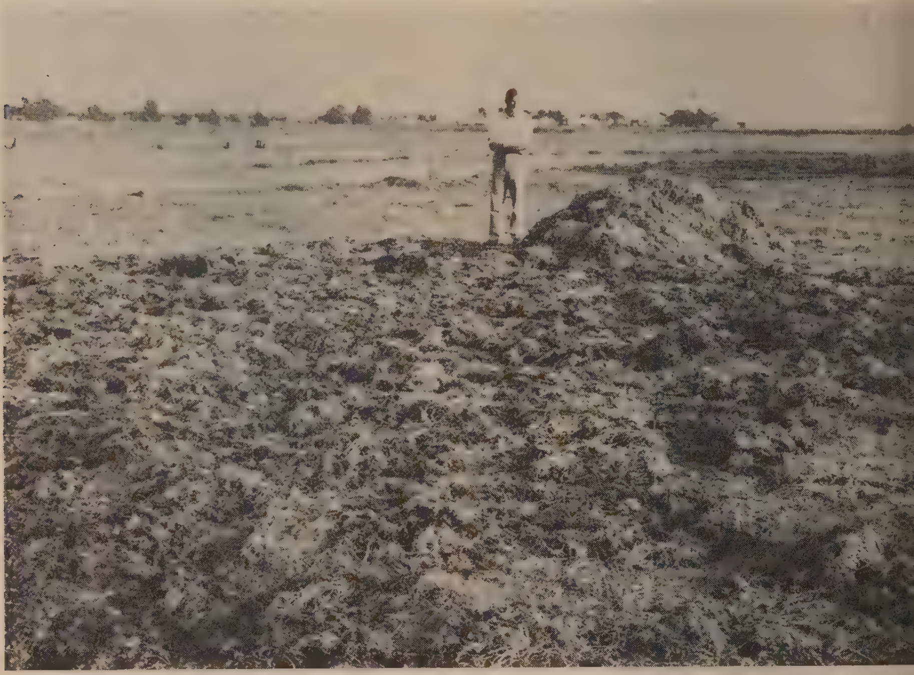

FIG. 8. Drying agarweed (*Gelidium cartilagineum* var. *robustum*) near Newport Beach Calif. (*Courtesy of U. S. Fish and Wildlife Service.*)

On the Pacific Coast, besides *Gelidium cartilagineum*, other species of *Gelidium* have also been used occasionally in the industry. The name "hair-agar" is generally applied by the agar divers to *Gelidium nudifrons* and sometimes also to *Gelidium arborescens*. These have thin and hair-like filaments, hence the vernacular name. They grow in deep waters, as does the agarweed, although in somewhat more sheltered places. They form bushes about three feet in height, and have to be harvested by diving and hand-picking. While they produce a slightly inferior agar, they are considered satisfactory agar sources. As they do not grow as luxuriantly as the agarweed, they are only occasionally gathered. In the drying field and in the factory they are generally mixed indiscriminately with the agarweed.

Two other species, *Gelidium densum* Gard. and *G. ramuliferum* Gard., have also been reported to be used by the California agar manufacturers, though apparently not in recent years, for the writer has never found any in the California agar firms. While there are several species of *Gelidium* on the Atlanti Coast, they are all too small for industrial use and not available in commercia quantities.

Agarweed Production. Production o agarweed on the Pacific Coast is rathe irregular, since diving is a hazardou and tiresome profession, especially diving for agarweed which has to be pulle from the rocks. Moreover, in places where the agarweed abounds, abalone is also found in large quantities, and experienced divers generally prefer to take up the more remunerative abalone diving. Furthermore, an agar diver can work only six or seven months a year, since it is not feasible, because of heavy ground swells, to work under sea during the winter and spring months. Consequently in California very few people are willing to take up agar diving as a profession. In Baja California, Mexico, the conditions are somewhat better, as agar diving is comparatively a better job than others there. The agarweed also grows more luxuriantly in the Mexican waters, and harvest per work day is higher than in California.

Monthly records of agarweed harvested in southern California from 1942 through 1944 are available through the kindness of the California Division of Fish and Game and are presented in the following table:

TABLE V

MONTHLY AGARWEED PRODUCTION IN SOUTHERN CALIFORNIA, 1942–44, IN POUNDS, WET WEIGHT

Month	1942	1943	1944
January	....	15,737	1,540
February	....	200	11,861
March	....	21,798	14,114
April	....	.. .. . .	....
May	10,700	2,453	12,102
June	46,000	10,675	38,869
July	41,000	25,491	106,287
August	29,400	102,880	96,222
September	6,085	21,337	51,515
October	9,243	13,326	125,156
November	30,622	7,462	21,295
December	42,676	....	3,260
Total	215,726	223,359	482,221

The monthly fluctuation of the harvest does not necessarily reflect upon the abundance of the weed in the various months, since the amounts gathered depend mostly upon the number of divers engaged in the work and the number of days when the sea was calm enough for agar diving. If we take the 1944 figure as a more representative one for normal production of agarweed in southern California, it is equivalent to about 240 tons wet weight, about 80 tons dry weight. Of these, about 27% came from the coast between Newport, Laguna and Dana Point, about 70% from Redondo and Point San Vincente, and the remaining from La Jolla and Point Loma, San Diego, based on figures supplied by The American Agar and Chemical Company, the largest agar producer in America.

The agarweed resource of the southern California waters is undoubtedly many times the 80 tons actually produced in 1944, since harvesting was then limited to only a few places readily accessible to diving boats. Wartime restrictions prevented operations in numerous places. Even in places where agarweed was gathered, probably more gelidium was left than was harvested. There are reasons to believe that southern California, if thoroughly but judiciously exploited, could yield upwards of 500 tons of dry agarweed per anum.

The majority of gelidium used in industry comes from Baja California, Mexico. While data of the Mexican production are not available to the writer at this moment, they can be easily calculated from the actual agar production and from the amount of agarweed harvested in California. The 1943 production of agar in California was 165,954 pounds, and on the average yield of 18 pounds of agar per 100 pounds of dry agarweed, the amount of raw material required will amount to 920,000 pounds or about 460 tons. Since southern California produced in 1943 only 223,359 pounds of wet gelidium, equivalent to about 40 tons, dry weight, the Mexican production should be about 420 tons, or about ten times the California production.

Gracilaria. Of the numerous species of *Gracilaria, G. confervoides* is the species most extensively employed in agar manufacture. It is, however, only in recent years that the value of this species as a commercial source of agar has been duly recognized and well established. It has been used for years in Japan in making agar, but it has always been a secondary source, used merely as a supplementary material. The recent research conducted in America by Humm and in other countries, including Australia and South Africa, has definitely shown that *Gracilaria* has its appropriate place in agar manufacture. Extraction of agar from *Gracilaria* has now passed from the experimental stage to large-scale commercial production in Beaufort, North Carolina, as well as in Australia and South Africa.

This agarophyte has a bushy frond attached by a discoid holdfast to stones, pebbles, shells, *etc.* The plant body is repeatedly divided, alternately branched, with numerous lateral proliferations. The branches are cylindrical throughout, 0.5 to 2.0 mm. in diameter, tapering gradually above and more abruptly below. The plant is dull purplish-red to purplish, grayish or greenish translucent. It grows best in sheltered bays, especially near river estuaries, where the water is shallow, the bottom sandy to somewhat muddy, and the water movement very sluggish. Under good environmental conditions, in most places, it grows five to six feet long in one season. At Beaufort, N. C., loose pieces of *Gracilaria* have been known to increase ten times in weight within two weeks. At Cherry Point, Vancouver, British Columbia plants 12 feet long are not uncommon.

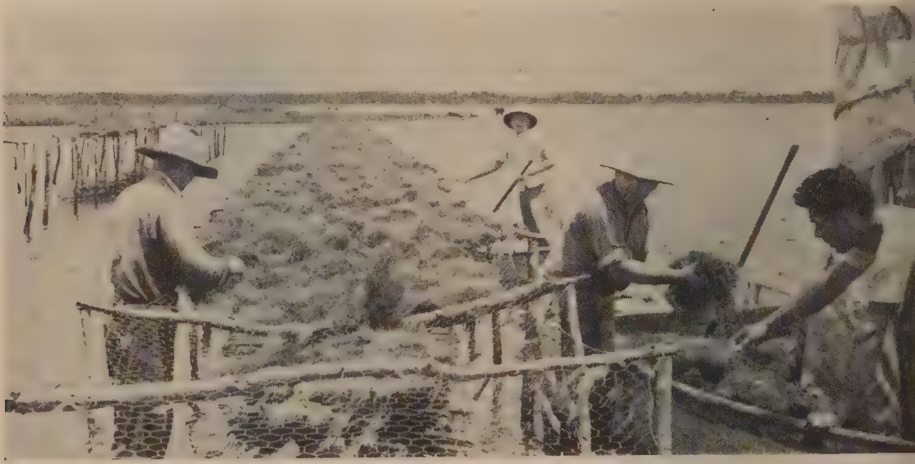

FIG. 9. Spreading agarweed (*Gracilaria confervoides*) on wire netting erected a few fee above the water surface for sun drying near Beaufort, N. C.

In places where *Gracilaria confervoides* occurs in commercially harvestable quantities, it generally grows an accumulates in great loose masses. Harvesting gracilaria is therefore a ver much simpler matter than harvestin *Gelidium cartilagineum.* It may be collected by forking it into small boats o hand-picked when the tide is low enough The wet gracilaria may be sent directl to the factory for agar processing, or ma be dried in the sun on wire netting erected a few feet above water. Humm reported that between August 1, 194 and January 1, 1944, 1,000 to 1,500 ton f wet gracilaria were gathered in the icinity of Beaufort, North Carolina. 'his was estimated to be equivalent to 50,000 to 200,000 pounds of dry gra- ilaria, or about 75 to 100 tons.

Gracilaria confervoides is a widely istributed, cosmopolitan seaweed, and rows in sheltered shallow bays where he water temperature is considerably aised by solar radiation. It is found xtensively, therefore, along both coasts. n Indian River, Florida, a variety of his species grows luxuriantly, forming arge mats on the eastern side of the bay. 'o quantitative data are available, but pparently the quantity available is nuch more than that in the Beaufort egion, or other places that the writer as investigated. *Gracilaria confer- oides* is also abundant along the Gulf f Mexico coasts, although no effort has et been made to determine its produc- ion there.

On the Pacific Coast this species forms eds in San Diego Bay at Chula Vista, 'alifornia. The productive area is, how- ver, relatively small. and this particular ed is probably able to supply about 100 ons of fresh gracilaria per annum, or bout 15 tons, dry weight. Because of he lack of extensive shallow sheltered ays in southern California, the writer vas unable to locate any other gracilaria eds besides the one at Chula Vista. 'his species apparently thrives as far orth as the east coast of Vancouver sland, British Columbia, where it grows o over 12 feet in length. Growth is ather sparse, however, and commercial xploitation does not appear to be easible.

Besides *Gracilaria confervoides*, *G. oliifera* is also utilized in agar manu- acture in the Beaufort, N. C., region, ut is considered inferior to the former n quality. It generally appears in early ummer, just before *Gracilaria confer- oides*. On the Pacific Coast, another pecies, *G. Sjostedtii* Kylin, grows in large quantities on rocks on sandy beaches, and might also be utilized in the industry, if extensive beds could be found.

Carrageens. The name "carrageen" is derived from the coastal town of Carragheen in the Irish Free State, and referred originally to the seaweed *Chondrus crispus,* more popularly known as "Irish moss". The term is now also applied to *Gigartina stellata* (Stackh.) Batters which is commonly harvested together with the Irish moss and used for similar purposes. It has been suggested, therefore, to use the term "carrageen" in a generic sense to include both *Chondrus* and *Gigartina,* and to limit "Irish moss" exclusively to the former.

Irish moss. Chondrus crispus is a bushy plant with several blades from a disk-like holdfast, generally 8 to 15 cm. tall, forming loose or often dense clumps. It has a slender compressed stalk which expands sharply into the wedge-shaped base, dividing dichotomously into a flabellate blade. The individual segments vary a good deal, some linear-compressed, some narrow band-like, and some broad-membranous, their breadth varying from 2 to 15 cm. The color of the plant ranges from dark red-purple when shaded or growing in deeper waters, to greenish when growing in shallow places.

Irish moss grows throughout the year on rocks, shells or woodwork in tide pools and in the intertidal regions down to 15 feet or more in depth. The usual method of gathering the "moss" is to hand-pick it when the tide recedes, or to rake it from below the water. In America the harvesting method is essentially the same as that of a hundred or so years ago.

A "moss" harvester does not require much equipment. He needs a 12-foot dory, a pair of oars, a rake, some crude fish oil, an anchor and a creel to carry the harvest from the dory to land. The rake is the only special equipment needed. It consists of a wooden handle, 15 to 20 feet long, and a steel strap, measuring 12 to 15 inches across and having 24 to 28 teeth. The teeth are six to eight inches long, made from quarter-inch, square steel tapered towards the outer end, and set, usually by electric welding, about one-eighth inch apart. The handle is set at an angle of about 75 degrees to the teeth. In harvesting the "moss", the rake is drawn with the teeth parallel to the bottom along the seaweed bed. The stems of the plant slide between the teeth and are held tightly there. The rake is then lifted and the "moss" pulled out and thrown into the dory. When the water is rough some fish oil is poured on the sea to improve visibility, thus helping the harvester to locate the seaweed beds.

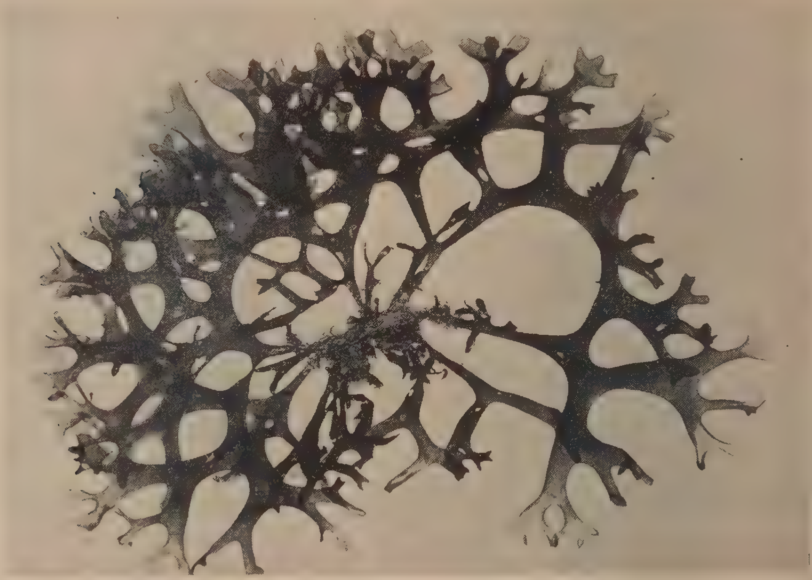

FIG. 10. *Chondrus crispus*, the Irish moss or carrageen of commerce, the collecting of wh
constitutes the oldest seaweed industry in the United States. For a century it has been harves
and sold, chiefly for making blancmange. Lately, a commercially useful extract, carrageenin,
been prepared from it, to serve as a stabilizer in chocolate milk, salad dressings, soda fount
syrups, cough syrups, tooth paste, hand lotions, and other products. (*Courtesy of Dr. William*
Taylor, of The Scientific Monthly and of the Journal of The New York Botanical Garden.)

Harvesting is conducted about t
hours before and after the lowest ti
An average harvester during this peri
can gather about 400 pounds of w
Irish moss. Under extremely favoral
conditions as much as 1,200 pounds c
be harvested by a single person in a da
Upon returning to the shore he packs
harvest in the wooden creel and carr
it to the drying fields or sells it imme
ately to the brokers.

Irish moss should be cleaned and dr
as soon as possible to prevent fermen
tion, which will produce a poor produ
and should be thoroughly washed fr
from shells, stones and the various ty
of animals accompanying it. Unc
First Cliff at Scituate, Mass., the ope
tors are equipped with a big tank a
two motors for curing the seaweed. C
motor controls the continual flow

ater pumped from the ocean which prays the "moss" in the tank, and the ther turns the giant paddles that beat e plant. From the vat the seaweed escends to a picking table of steel mesh at runs as an endless belt. Here the moss" is separated from the crabs, eriwinkles, rock eels, *etc.,* that do not ome out in the vat. The cleaned Irish oss is then transported to the drying oards, canvas or wire netting. It is inly spread, bleached and dried in the n.

Irish moss is produced in several Euro- ean countries, especially Ireland, Scot- nd and France. Before the war most f the carrageen and its extract sold in merica came from these three sources. fter the war in Europe started, both e United States and Canada acceler- ted their production which may now ex- eed the total European output.

On the American Atlantic Coast, lthough *Chondrus crispus* occurs from ew Jersey to Newfoundland, only cer- ain regions have large enough quanti- ies to support commercial harvesting. n the United States, Massachusetts and aine are the two carrageen-producing tates, and Scituate, Mass., is still the enter of Irish moss production, which s affording a livelihood for at least 300 ocal people. Gloucester and Quincy, nd to a less extent Lynn and Nahant n the same State, are also producing this eaweed. According to one processor, roduction of Irish moss in Scituate and earby regions was expected to reach alf a million pounds dry weight in 1946.

Chondrus crispus is reported to be bundant along the entire length of the aine Coast. Although the Maine Irish oss industry is comparatively young, t is estimated by one processor to have roduced two million pounds of the fresh eaweed, or close to 400,000 pounds of he dry plant in 1944. The present an- ual United States production is esti- ated by two of the largest producers t about five million pounds of fresh or close to one million pounds of dry Irish moss. Irish moss costs about $40 per ton when fresh and about $400 when dried and bleached.

In Canada the greatest quantity comes from Prince Edward Island and the mainland from the Gut of Canso to Malagash and from Richibucto to Point Escuminac, in the southern part of the Gulf of St. Lawrence. Large quantities also come from the outer coast of Nova Scotia, with good producing grounds in Yarmouth County. The annual Canadian production rose from the prewar 10,000 pounds to 261,000 pounds in 1941, and 2,006,000 pounds dry weight in 1942. The 1943 production was only 877,000 pounds, a figure based on shipment records. One authority believed that over 1,200,000 pounds were actually produced in 1943. The smaller production in this particular year was assumed to be due to the excessively large purchase in 1942, so that buyers were very critical about the quality of the product, and refused to take inferior materials. Current annual production is about two million pounds.

Gigartina. Before the last war in Europe, one carrageenin producer in the United States imported annually for several years about 15 tons of the so-called "Portuguese moss". This consisted of three different seaweeds. "Portuguese moss, wiry type" is *Gigartina acicularis* (Wulf.) Lam., and "Portuguese moss, wide-leaf type" is a mixture of *Chondrus crispus* and *Gigartina stellata.* As the "wiry type" is a more important constituent of the "Portuguese moss", the name should be restricted to *Gigartina acicularis.* This gives a colloid similar to, if not identical with, the Irish moss carrageenin. The Portuguese moss colloid, however, gives a much more viscoid solution than that from Irish moss, and is used for certain special purposes.

Although *Gigartina stellata* is almost as abundant as the Irish moss on the

northern European coasts, this species does not appear to be available in sufficient quantities on the American side of the Atlantic to warrant commercial harvesting. Among commercial samples of American Irish moss, *Gigartina* is indeed a rare component. On the Pacific Coast there are several species of *Gigartina*,
one of which, *G. corymbifera* Kuetz
occurs along the central and norther
California Coast in sufficiently larg
quantities for commercial exploitatio
It contains a colloid of excellent stab
lizing power, probably identical wit
carrageenin from Irish moss. This se
weed is a broadly membranous for
with thick and tough blades reachin
two to three feet in length. It grow
profusely on rocks at or below low tide
and has to be collected during sprin
low tides. Collecting is not difficul
however, and the writer once gathere
about 80 pounds in about 15 minute
It is not improbable that *Gigartin*
corymbifera may eventually find an a
propriate place in America's carrageeni
industry.

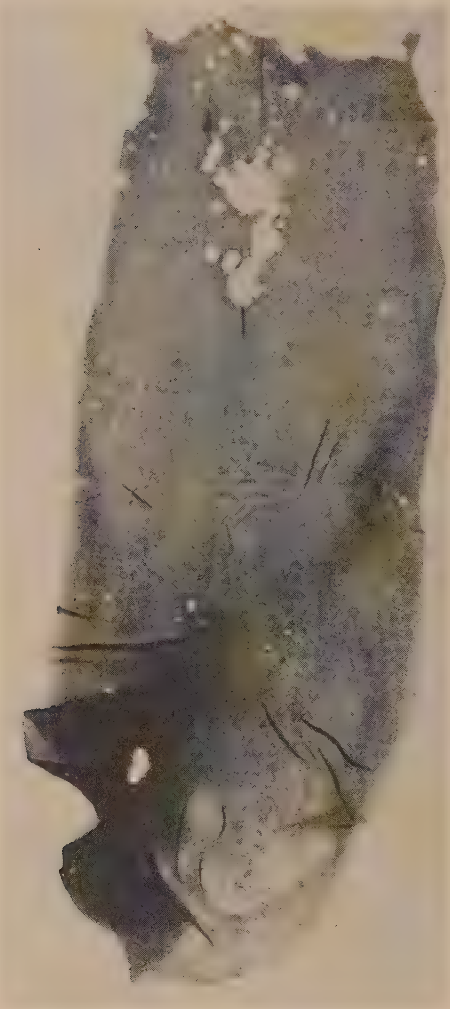

FIG. 11. *Iridophycus flaccidum,* source of the phycocolloid, iridophycin, a newly introduced colloid in stabilizing chocolate milk. (*Courtesy of the New York Botanical Garden.*)

Other Red Seaweeds. The red se
weeds now used in America beside
Gelidium, Gracilaria, Chondrus an
Gigartina are *Iridophycus, Porphyr*
and *Rhodymenia.*

Iridophycus. Two species of th
genus are utilized, namely, *I. flaccidu*
and *I. splendens.* They yield a colloi
iridophycin, which has properties sim
lar to those of carrageenin. Both sp
cies have lanceolate or ovate-lanceolat
blades with short stipes, arising fro
disk-shaped holdfasts. The thalli ar
soft in texture when fresh, turning toug
and rubbery when dry. *I. flaccidu*
reaches two feet in length and is gree
ish-olive when growing in the mid-li
toral, deep purple in the lower littora
I. splendens reaches four feet in lengt
generally grows in deeper waters tha
the former species and is of a rich pu
ple in color. Both grow on rocks som
what sheltered from the surf. Comme
cial iridophycus comes from near Cre
cent City, Pt. Arena, and Jenner i
California, and south of Coos Bay i
Oregon. Harvesting season exten
from June to December. The plants a
picked by hand from the rocks at lo
tide, and during one low tide, lasti

rom two to three hours, one man can ick from 200 to 300 pounds of the fresh eaweed in favorable locations. A good icker is known to have gathered as uch as 400 pounds in one tide. Much epends on the location, the tide, and specially on conditions of the sea as a esult of the velocity and direction of he wind. There are many beaches with xcellent growths of *Iridophycus*, but nfortunately they are inaccessible by and. Commercial gathering started in he summer of 1944. In 1944 and 1945 bout 14 tons of the fresh seaweed were arvested from California and about 16 ons from Oregon. The 1946 production vas expected to be over 30 tons. *Irido- hycus* dries to about 22% of its weight vhen freshly harvested. It costs about ive cents per pound to gather the fresh veed, or about $100 per ton. A ton of he sun-dried iridophycus will therefore e worth around $700, considering expenses involved in drying, in addition to harvesting cost. There is only one firm engaged in processing iridophycin. It buys the fresh seaweed and takes care of the drying itself.

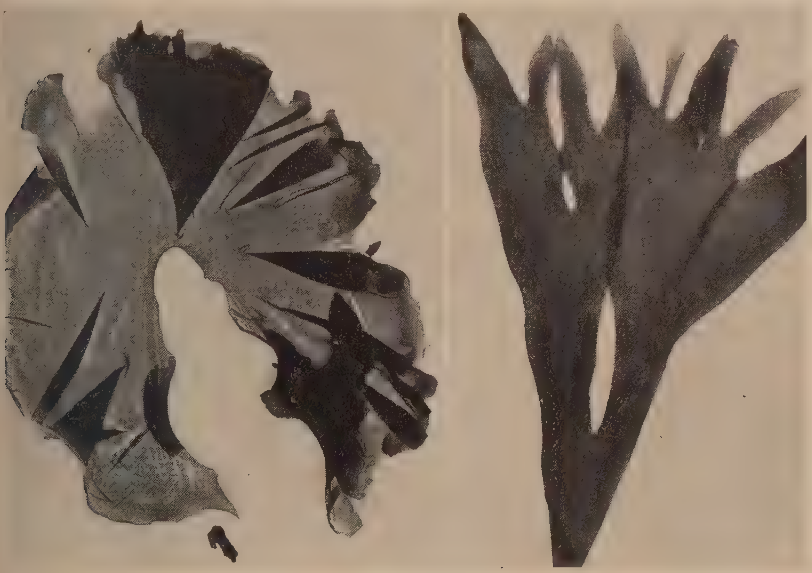

FIG. 12. Two American food seaweeds, California or purple laver (*Porphyra perforata*, left) nd East Coast dulse (*Rhodymenia palmata*, right). Indians of the Pacific Coast relish the laver, nd the Chinese use it in their seaweed soup. In eastern metropolitan markets dulse is occasionally n sale, to be eaten raw as a relish. (*Courtesy of the Journal of The New York Botanical Garden.*)

Porphyra. While most species of *Porphyra* may be utilized as food, the species commonly harvested is the perforated laver, *Porphyra perforata* J. Ag., of California. This forms large, brownish-purple, deeply lacinate, lanceolate to irregularly shaped membranes with deeply ruffled margins. The blades may reach five feet in length, but generally are about two to three feet long. The laver grows on rocks in rather sheltered places from the mid-littoral to the limit of high water. Bonnot reported that 300,000 pounds of dried laver were harvested in 1929 by white men and Indians in northern California and by Chinese in central and southern California. The Chinese harvesters usually come to the laver grounds in the fall and burn, with driftwood, the rocks on which they expect their laver crop to grow. By early spring these rocks are densely covered with the *Porphyra.* In harvesting, the laver is merely pulled from the rock by hand and is dried in the sun in the form of rectangular sheets. At present, California laver is worth $600–800 per ton.

Rhodymenia. American dulse is *Rhodymenia palmata* (L.) Grev., found along the Atlantic shores from North Carolina northward. Most of it comes from the Canadian Maritime Provinces, especially from the Bay of Fundy, where it grows on rocks in the low littoral and is harvested by hand picking during spring low tides. No data are available as to its production.

Utilization of Seaweed Products

In America, as elsewhere, there have been three stages in the development of the utilization of seaweeds and their products. During the first stage, seaweeds were merely gathered, dried and employed as food or medicine without other processing. In America this started about a century ago with Irish moss as the first seaweed thus utilized. At present we have, besides Irish moss, edible kelp from *Nereocystis,* laver of the West Coast and dulse of the East Coast. Perhaps we should also include kelp meal which is made into stock feeds or tablets for humans. In the second stage of development seaweeds were utilized to supply non-colloid chemicals and had to be processed to yield these products. This started just before World War I, flourished during the war, and came to an end a few years after the war. It was short-lived, but it had reached, within a few years, a stage of glory not matched by even the seaweed industry today. During this period, high grade potassium chloride, acetone, calcium acetate, iodine and decolorizing carbon were produced in large quantities from the California giant gelp, *Macrocystis pyrifer*
At present these materials may be o
tained more cheaply from other source
and seaweeds are no longer used
America as raw materials for non-collo
chemicals. In the third and most rece
stage, interest in seaweed utilization h
shifted to the seaweed colloids, or phyc
colloids. They are extremely valuab
as gelling, suspending, emulsifyin
thickening and body-producing agen
and have found extensive uses in foo
drugs, cosmetics and other industri
products.

Commercial production of seawe
colloids started during World War
when algin was made at San Diego as
by-product in the kelp industry. Algi
however, did not become the princip
kelp product until the late 1920's a
early 1930's. Agar, another importa
colloid, was first made in Tropico (no
Glendale), California, in 1920. Althou
the colloid of Irish moss has been in u
for over a century in making blan
mange in the New England states, it w
not until the late 1930's that it beg
to be produced in the present purifi
powdered form. Large commercial pr
duction of carrageenin actually start
in 1942. Iridophycin was made in co
mercial quantities in 1945; its produ
tion at present is still small in compa
son with that of the other phycocolloi
Uses of seaweed products in Ameri
have been discussed also elsewhere.[1]

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[1] Commercial Intelligence Jour. 67: 129, 40
1942.
Smithsonian Inst. Rep. 1941: 401. 1942.
Fish. Market News 5(6): 1. 1943.
Bull. U. S. Bur. Fish. 24: 167. 1905.
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230, 232, 234, 258, 259, 356, 358. 1945.
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1946.
Phycocolloids: useful seaweed polysacch
rides. *In* Jerome Alexander, Colloid che
istry, theoretical and applied. Vol 6. 194

Non-Colloids. There are two general oups of non-colloid seaweed products, red seaweeds and ground seaweeds. ured seaweeds are sun-dried, sometimes rtially bleached, and are used in the rm of whole plants. They chiefly serve r food or in making food preparations, d include bladder kelp, laver, dulse d Irish moss. The bladder kelp was ed in the last war as a kombu (Japa- se kelp) substitute by the Japanese in e United States, and the Chinese use ver extensively in their so-called sea- eed soup. Dulse is eaten raw and dry a kind of salad or relish, or is em- oyed as a thickener in soups, sauces d gravies. Use of Irish moss in the eparation of the well-known blanc ange has been centuries old on the ast Coast, and for its preparation the llowing directions have been given:

“Soak half a cup of dry moss in cold ater for five minutes, tie in a cheese- oth bag, place in a double boiler with quart of milk and cook for half an ur; add half a teaspoonful of salt or ss, according to taste; strain, flavor ith a teaspoonful of lemon or vanilla tract if desired, and pour into a mold small cups, which have been wet with ld water; after hardening, eat with gar and cream.”

Stock feed. Ground seaweed is made tirely of kelps, from both macrocystis d nereocystis, hence generally called lp meal. Its principal use is as stock ed, and analyses of it show the pres- ce of large amounts of various min- als as well as vitamins A, B, F and G. ne company produces a meal consisting tirely of dried and ground macro- stis, while another concern uses the me plant but mixes it with fish meal and fish press-water concentrate, fortified with various beneficial substances. There are four kinds on the market under the trade name “Manamer”, one for hogs and pigs, one for chickens, one for horses and one for cattle. These are all supplementary feeds to be mixed with grains and other established rations.

The value of seaweeds as stock feeds has been quite well established. Along the coast, the seaweeds may also be used *in toto*. They should, however, be rinsed in fresh water to leach out the excessive salts which, if taken in large quantities, may have an adverse effect on the health of the animals. It has also been found in Europe that animals may require from a few days to a week or more to readjust their food habits from an ordinary ration to a predominantly seaweed diet. The value of seaweeds as stock feed differs with the kind of plant used, with the season of harvesting, with the different animals feeding on them, and with the individual preferences of the animals for the kind offered as food.

Medicinal tablets. Kelp meal from macrocystis is also made into tablets for human consumption to supply mineral salts needed by the human system. There are at least three concerns engaged in this trade. One company at Anacortes, Washington, makes the meal from the bladder kelp in the Puget Sound region, and sends it to New York for processing into kelp tablets. At Vancouver, British Columbia, a new kelp company was recently formed to utilize local kelp resources for similar and other purposes. Kelp meal is also used as a constituent in the diet of hatchery-reared fingerlings at Seattle, Washington, being employed on a basis of 2% of the weight of the ration fed.

Manure. Utilization of seaweeds as manure in America, as elsewhere, has been centuries old. In Rhode Island, for instance, as late as the 1890's, seaweeds formed an important source of farm

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Textile Age. 1946.

Nat. Mag. 36(3): 127. 1943.

Cal. Fish and Game 28(4): 199. 1942.

Marine products of commerce. 762 pp. 1923.

manure, and in recent years, kelps have been used in various coastal regions as fertilizer. Farmers living at Encinitas, California, gather the drifted kelps on the beach to fertilize their avocado orchards. One chief obstacle in using whole seaweeds as manure is the bulkiness of such materials which contain more than 95% of water. Since the drying and grinding processes do not decrease the value of kelps as fertilizer, use of kelp meal eliminates this trouble. It is expected that kelp meal may eventually be marketed as regular manure for special types of crops.

Colloids. As already mentioned, there are produced in America, at present, four kinds of phycocolloids, namely, algin, agar, carageenin and iridophycin. Of these, algin comes from the brown seaweeds, the other two from red seaweeds.

Algin. The term "algin" generally refers to the sodium salt of alginic acid, a polyuronic acid composed entirely of d-mannuronic anhydride residues. Like the other seaweed colloids of commerce, algin is useful wherever a hydrophilic colloid possessing marked gelling, suspending, emulsifying, thickening and water-holding properties is required. Unlike the other phycocolloids, it is chemically active, reacting readily with various metallic salts and acids. Consequently, in certain respects, its uses are limited, while in others it serves especially well by virtue of its reactivity. For example, many of the present industrial uses of algin are based on the fact that addition of a calcium salt to an algin solution produces an immediate precipitate of gelatinous calcium alginate. Thus, by the controlled release of calcium ions, through the use of a relatively insoluble calcium salt, such as calcium citrate, the solutions may be either thickened or converted into rigid gels, in accordance with the amount of the calcium salt added. The rate of the setting of the gel may also be controlled by the introduction of salts, such a
soluble phosphate, which form calci
salts more insoluble in water than
cium alginate.

In the preparation of algin soluti
for use in food and other industr
water should be warmed to about 1
F. and the solution should be vigorou
stirred. Algin solutions are suscepti
to bacterial growth. Therefore, p
servatives are commonly added to th
if they are to stand for prolon
periods.

The most important use of algin
undoubtedly in stabilizing ice crea
where a colloid is needed to imp
smooth body and texture and to prev
formation of large ice crystals dur
storage. It is prerequisite that suc
stabilizer will not in any way mask
flavor of the resulting product.
cream mixes made with efficient sta
izers, whip fast and produce suffici
overrun. Such ice creams show a smo
clean meltdown without any se
drainage or wheying off. Previou
gelatin was the sole standard ice cre
stabilizer, but since algin was introdu
about ten years ago, it has been ra
by most experts as a better material t
gelatin. At least 50% of the facto
made ice creams in the United States
now stabilized with algin.

Some years ago algin was used ex
sively as a chocolate milk stabilizer.
recent years, however, carrageenin
become the most important agent
this purpose, and while some algin is
being used, it is always employed
gether with some carrageenin. U
very recently, orange and lemon
have been stabilized almost exclusi
with gums, but algin is now successf
used for the same purpose. It also
the role more satisfactorily in st
lizing sherbets, where the more co
agar, which required a higher temp
ture to dissolve, was previously u
To reduce serum drainage, algin is

ito cream cheese and cheese spreads and
lso whipping creams for decorating
ancy cakes. It also serves as a gelling
gent in milk puddings by virtue of its
eaction with calcium in the milk. Algin
also employed in many different ways
food preparations, such as jellies,
ms, icing, meringues, fillings, milk
owders, oleomargarines, candies, fruit
ice powder and sausage casings.

Algin is useful also in pharmaceutical
reparations, emulsifying the petrolatum
ase, for instance, in making sulfanila-
ide ointments for surface wounds. It
rves as a constituent in pills and tab-
ts, and is also used occasionally in
nulsions to carry medicinals such as
tamins. In the cosmetic industry algin
now considered to be one of the most
seful colloids, its value residing in its
bility to produce standard preparations
controllable consistency, which are
ansparent, water-white and almost
lorless. Ordinary preparations made
ith karaya gums, for instance, have a
ayish-brown color, and those made
ith tragacanth are quite opaque. An-
her advantage of algin preparations is
e wide range of controllable viscosity,
fected by the addition of calcium ions
sodium alginate solutions. The prepa-
tions may either be thickened to
eams or converted into jellies, depend-
g on the amount of the calcium salt
lded. It is an excellent vehicle for
nd lotions of the saponified type, and
valuable base for tooth pastes and for
easeless, water-soluble ointments and
bricating jellies, replacing tragacanth
d other gums, because it is compatible
ith most of the ingredients in the of-
ial formulas.

Sodium and ammonium alginates are
th used extensively in the preparation
vehicles for resin emulsion paints, the
gin serving as an emulsifier. Algin
ssolves shellac to form a lacquer which
ies to a tough, tenacious film. Treat-
ent with dilute acids or calcium chloride solution renders this film insoluble, hence useful as a water-proof varnish. Coated over asphalt paints for steel plates and insulated wires, algin helps to prevent the painted surfaces from adhering to each other. During the last war, algin was used as a stabilizer for camouflage paints. Copper alginate serves as a dressing for canvas and burlaps to prevent mildew. Algin is used in the preparation of a new type of fire-retarding compound, recently developed at the United States Forest Products Laboratory. This consists of finely ground fire-retarding chemicals dissolved and suspended in an aqueous sodium or ammonium alginate solution. Best results are obtained with monoammonium phosphate as the fire-retardant, although a mixture of borax and boric acid also gives satisfactory results.

In dentistry algin serves as a dental impression material. Algin-based preparations do not produce as accurate molds as do the traditional agar-based ones. They are, however, more convenient to use and are therefore extensively employed by dentists for general work. Recently ammonium alginate has been adopted for coating dentures made of acrylic resin to take the place of tinfoil which has not been available for this purpose because of the war. Two coatings of the alginate solution are applied with a brush to the gypsum molds when these are still warm from the wax removal. When dry they are immersed in calcium chloride solution, thus converted *in situ* into insoluble calcium alginate coatings. Use of algin in coating dentures is easy and gives very uniform results, and is expected to continue even when tinfoil comes back in sufficient quantities.

In the rubber industry algin serves as a latex-creaming agent; for this purpose ammonium alginate is used instead of the sodium salt. Algin is also useful in treating boiler water for preventing incrustation. It reacts with the calcium salts, forming globular flocculent precipitates; these envelop other sediments to give a soft pasty sludge which can be readily blown out of the boiler at regular intervals. As a sizing material algin has the advantage over starch in that it fills the cloth more completely, is tougher and more elastic. In printing pastes algin is widely used as a thickener. Triethanolamine alginate, an algin derivative, is employed as a coating material for solid surfaces. Incorporated in insecticide sprays, algin activates and greatly reduces the necessary effective chemical. Algin is also employed in the purification of beet juices in sugar manufacture, in oil-well drilling muds to seal off porous formations, as a medium for separating plates in the manufacture of storage batteries, as a binder for printer's ink, in the finishing of leathers, and in the preparation of a color-absorbing material.

Agar. Chemically the sulfuric ester of a linear galactan, agar consists of a long chain of *d*-galactopyranose residues, terminated at the reducing end by one residue of *l*-galactopyranose. It is a valuable colloid principally because of its strongly hydrophilic nature and its high gel-strength quality. It is used where bulk is wanted, or where a suspending, stabilizing, thickening or gelling agent is desired. An important use of agar is as roughage. Being not digestible in human systems, agar, when taken in the form of powder or flake, serves as a bulk-producer. This problem of bulk supply is one that only civilized man, accustomed to highly refined food, has to encounter, and agar flakes successfully take the place of the coarse materials that his ancestors ate normally with every meal. For similar reasons agar is incorporated in certain types of breakfast feeds and special bakery products for victims of constipation.

Because of its moisture-holding ability, agar is extensively used in making fr
cakes. These are generally prepa
weeks before they reach the custom
and the addition of agar helps to k
them in good condition for a long per
Agar is used in stabilizing icings,
making chiffon pies, in meringues
fillings. It is employed in making
fectionaries, chiefly in jelly candies
marshmallows, and in preparing mal
milks and acidophilous milks. It
serves as a thickening and gelling ag
in the canning of pickled tong
poultry and the softer types of meat
fish.

Agar is a constituent of petrole
agar emulsions. In such preparati
however, it does not serve as a laxat
as the public is led to believe, since
present in too small a concentrat
generally less than 1.5%, to be effect
It serves primarily as an emulsifier
helps to make the preparation easie
take. Agar is employed as a vehicle
lactic acid to combat toxicogenic bact
in the intestines. An interesting us
medicinal preparations is in the so-ca
"seal-ins" for pills, a type of coa
which regulates the rate of solutio
the capsule and consequently the tim
of its opening. The agar is adde
tiny particles and distributed in
waxy material of the coating. By vi
of its water absorption, agar assist
the release of the coated medicinal pr
ration in the desired place. Agar is
used in the coatings of certain gen
violet capsules employed in the t
ment of infection with *Oxyuris verm*
laris. It is also a constituent in a pr
ration for the treatment of Coccidio
infection in chickens.

Agar is best known, however, as
standard material in the preparatio
solid microbiological culture media,
as such, is an indispensable materia
the routine sanitary analyses of w
and milk. Its importance in pu
health work and medical and scien

earch is so significant that during
orld War II the United States Govern-
nt had to freeze the available agar
pply so that the nation's health would
t be impaired by lack of this seaweed
loid. In scientific laboratories agar
ves as an embedding medium for
crotome sectioning, as a vehicle in the
ndard *Avena* test for plant growth
rmones, and as a coagulant for barium
fate precipitation. In agriculture
ar is useful as an insecticide activator
d carrier, and in making coatings for
rogen bacteria cultures.

Agar is extensively used in prosthetic
rks. It is the basic material in most
ntal impression materials. In highly
tical works, such as inlays and fixed
dges, agar-based compounds are prac-
ally the only materials used. Though
ar alone is unsuitable for use in cer-
n photographic materials because of
tendency to stick to gelatin and its
olubility in organic solvents or in
caline solutions, the esters of agar are
uble in a number of organic solvents
d can therefore be employed as coat-
gs or backings for photographic films,
m which they may be later removed
means of alkaline solutions. Back-
gs are required to keep the films flat
d, to some extent, to carry colored
terials for minimizing halation.

In the hot-drawing of tungsten wires
electric lamps a lubricant is neces-
y. At present the lubricant is an
ar gel in which powdered graphite is
chanically held in suspension. For-
rly the industry used an expensive
terial known in the trade as ‘‘aqu-
g’’, procurable only from limited
rces. The agar-based lubricant is not
ly relatively inexpensive and easily
ocurable, but also more efficacious.
e agar gel is able to hold in suspen-
n larger particles which, within cer-
n ranges of size, provide more com-
te and uniform protective covering
the exterior of the wire.

Shredded agar has been recommended to be incorporated in small amounts in tobacco to retard excessive evaporation of moisture. In hectograph duplicators, agar is used to make the gelatinous rolls. It is also used in the manufacture of submarine storage batteries.

Carrageenin. Like agar, carrageenin is the sulfuric ester of a galactan. It has additionally, however, a certain percentage of 2-ketogluconic acid. The most important use of carrageenin in America is undoubtedly that of stabilizing chocolate milk. Previous to the introduction of a stabilizer, the chocolate-flavored milk on the market always had a sediment of cocoa particles at the bottom of the bottle. The bottle, therefore, had to be shaken vigorously before the drink was poured. The sediment usually adhered so firmly to the containers that great difficulty was encountered in washing them. Now, with the addition of a small amount of carrageenin, these difficulties are largely eliminated. To make chocolate milk, a chocolate syrup is first prepared. The syrup is made by adding a mixture of cocoa, salt and carrageenin to invert sugar solution at about 190° F., and contains about 0.4% carrageenin. One gallon of this chocolate-flavored syrup is then mixed with 11 gallons of milk, and the mixture pasteurized and finally bottled. The finished product thus contains only 0.04% of the Irish moss extract; yet the cocoa fibers are effectively held in a homogeneous suspension and the butter fat does not rise to the top.

Carrageenin is used in food preparations in similar ways as agar and algin. It is employed extensively in making puddings, cheese spreads, pie fillings, cake frostings, jelly fillings, jams, preserves and candy. In the dairy industry, besides being the principal stabilizer in making chocolate milk, it is also employed in stabilizing ice cream, ices and sherbets, and its use in this respect is said to be increasing fast. It is used in emulsifying cod-liver oil as well as mineral oil. "Decoction Chondri" prepared from carrageenin is probably the best known phycocolloid pharmaceutical emulsifier. The National Formulary recommends a 3% Irish moss solution for the "Mucilago Chondri," which is used by itself as a demulcent and frequently as a vehicle for other medicaments. When employed as the base of cough medicines, carrageenin is said to give them body and to produce a slight soothing effect. It is reported that in Irish bar-rooms in New York, carrageen is soaked in whisky and the resulting liquor offered to patrons as a cough remedy. Carrageenin is also used as a granulating agent in such preparations as aspirin tablets.

In the cosmetic industry, carrageenin is extensively used as a binder, emulsifier, gel-former and bodying agent. It is a regular ingredient in many tooth pastes, and a thick mucilage is used in deodorant pastes. It serves as the base of sulfonated oil-curling jellies, and is also an ingredient of compact powders and rouges. It is employed in making glycerine jellies for chapped hands, and as vehicles for the saponified type of hand lotions.

During the last war, because of a shortage of agar, one concern made a special carrageenin preparation under the trade name "Carragar" to serve as an agar substitute in the preparation of solid microbiological culture media. This contains additional potassium salts which help the carrageenin to form a firmer gel, approaching agar gel. Normally, carrageenin by itself forms a weak gel, even at high concentrations. The product apparently is quite successful for certain media, but for the standard techniques, the excessive syneresis of Carragar media eventually interferes with the counting of colonies on plates.

Before liquor prohibition in the United States, one of the most important u of carrageenin was in the fining of be and ales. In the early stages of b brewing, the cloudy solution of malt tracts contains insoluble materials a undesirable proteins. These can be moved by natural slow setting or ra fining with the help of a clarifying age Carrageenin has the ability to comb with the tannin of hops to form a gela nous mass which absorbs the suspend impurities. The resulting floccul mass is easily removed as a scum. Car geenin is still being used in the liq industry as a clarifying agent, althou it has been partially replaced by ot chemical finings.

Carrageenin imparts to certain ty of leather a desirable gloss and stiffn It is principally used in the finishing straight grains and grain upper leath A solution is brushed on the leat which is then glazed by rubbing w glass cylinders. This mucilaginous s stance smooths and holds down the t rough projections on the surface of finished leather. In inner soles, ca geenin is used as a filler to impart s ness and body to them. Its use helps in the water-proofing of very he leather. When used in shoe polish leather dressing, carrageenin serves restore the finish to worn, scuffed leat and one shoe manufacturer in New E land alone used to import annually ab 12,000 pounds of Irish moss from land solely for leather finishing.

Like algin, carrageenin is extensi employed in making water pai Casein paints stabilized with it are ea applied and adhere well to the sur while drying. Carrageenin was am the first hydrophilic colloids used in creaming of rubber latex, althoug present ammonium alginate is the creaming agent from seaweed source

Iridophycin. Like agar and ca geenin, iridophycin is a galactan ethe sulfate, although of a much simpler itution. Its introduction to industry very recent, and its use is still limited stabilizing chocolate fibers in the eparation of chocolate milk. It is said be better than carrageenin when cold ix is used in making the preparation.

Laminarin and Fucoidin. There are least these two other seaweed colloids hich could be produced in commercial antities in America. However, there as yet no commercial applications for em, and hence attempts at commercial oduction of these substances have not en made by the industry.

Summary of Resources

Production of acetone, iodine, kelp- ar and potash from kelp on the Pacific ast of the United States as a result of orld War I has been superseded since e late 1930's by industries on both the lantic and Pacific Coasts that produce her products from seaweeds, namely, ar, algin, carrageenin and iridophycin.

The extensive industrial uses of these oducts can not be summarized beyond at has been done in the foregoing ac- unt without omitting some of the uses.

According to investigations made in e years 1911 to 1913, there were at that ne about 390 square miles of kelp beds th about 60,000,000 tons of kelp grow- g along the Pacific Coast from Cedros and, Mexico, to western Alaska. This imate has since been regarded as too gh.

These Pacific beds consist mainly of *crocystis pyrifera, Nereocystis Luetkeana* and *Alaria fistulosa.* The greatest recorded production from them in California was 394,974 tons of fresh kelp in 1917; the production of 1918 may have exceeded that amount. In 1945 a little over 59,000 tons were harvested.

The economically important kelps on the Atlantic Coast are *Laminaria saccharina* and *L. digitata.* Data are not available regarding the supply and harvest of them, but since about 300,000 pounds of algin were produced from them in 1944, and since algin constitutes about 4% of these kelps, the production that year was at least 4,000 tons, or less than 10% of the current Pacific Coast production.

The two principal sources of agar are *Gelidium cartilagineum* of the Pacific and *Gracilaria confervoides* of the Atlantic Coast. In 1944, 240 tons wet weight, 80 tons dry weight, of agarweed were recorded as having been harvested along the California Coast.

Carrageenin is obtained from *Chondrus crispus* (Irish Moss) and *Gigartina stellata.* The former abounds in commercial quantities along the Atlantic Coasts of both Europe and America; the latter only along the coast of Europe. Harvesting in America is centered around Scituate, Mass., and the production in 1946 was expected to reach half a million pounds dry weight.

Iridophycus flaccidum and *I. splendens,* both of the Pacific Coast, are the sources of iridophycin, a colloid with properties similar to those of carrageenin.

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EFFECT OF EARTH'S ROTATION UPON CONVECTION CELLS*

By Walter H. Munk

The Scripps Institution of Oceanography, La Jolla, California

Woodcock[1] has presented evidence that the Portuguese man-of-war is consistently driven to the left of the wind in the northern hemisphere, and probably to the right of the wind in the southern hemisphere. This peculiar behavior, he points out, improves the animal's chance for survival if it sails through water divided into asymmetrical convection cells, such as the ones he has measured in the North Atlantic and the Gulf of Mexico. In FIGURE 1, the vertical plane of the cells is at a right angle to the wind direction. An observer in the northern hemisphere looking down-wind would find the clockwise vortex better developed than the counterclockwise vortex. Woodcock suggests that this asymmetry is the result of the Coriolis force.

An exact dynamical analysis of the problem is difficult, but an estimate of the effect of the earth's rotation can be made with the aid of Bjerkness' circulation theorem. The circulation theory is usually written in the form

$$\frac{dC}{dt} = N - 2\Omega \frac{dA_e}{dt}, \tag{1}$$

where C is the circulation around a closed circuit, and A_e the area surrounded by this circuit, when projected upon the equatorial plane; N is the number of solenoids which are maintained by evaporation at the surface, and

$$2\Omega = 1.46 \times 10^{-4} \text{ sec.}^{-1} \tag{2}$$

is the double angular velocity of the earth.

Cyclonic circulation is taken as positive. The negative sign in EQUATION 1 means, therefore, that a growth of the convection cell tends to bring about anti-cyclonic circulation. If, for example, a circular disc were to rotate about an axis fixed to the earth's surface, and this

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disc were to expand, its rotation would lag increasingly behind that of the earth's surface. To an observer on the earth's surface, the disc would develop an anti-cyclonic rotation.

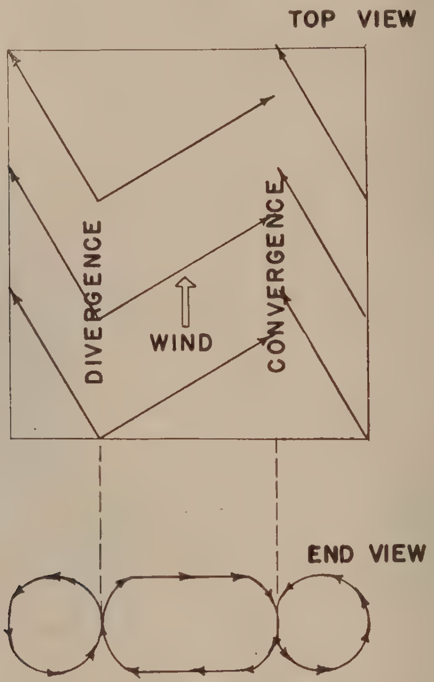
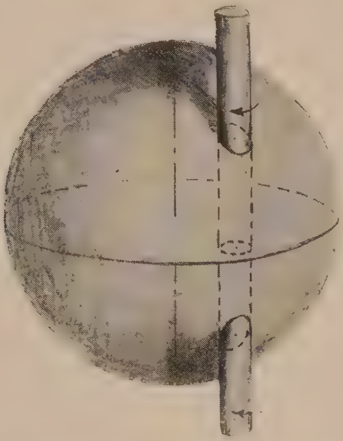


FIGURE 1. Idealized drawing of asymmetrical vortices, according to **Woodcock**, 1944.

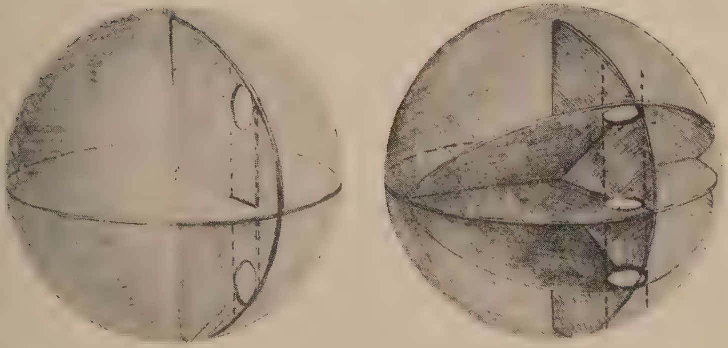
The growth of convection cells could perhaps be visualized in the following manner. As the wind first starts blowing, evaporation cools a thin surface layer, and the resulting instability stimulates the formation of vortices. There is, *a priori,* no reason why these vortices should be cyclonic or anti-cyclonic. But the cyclonic vortices, expanding under the sustained action of the instability forces (the solenoids N) must work against the inertial forces of the earth's rotation, and their development is retarded. Anti-cyclonic vortices are assisted in their growth by the earth's rotation. The final result is the development of full-scale anti-cyclonic vortices, separated by secondary cyclonic vortices.

This concept is in disagreement with Rayleigh's convection cell theory. according to which the dimensions of the cell are independent of the instability forces, and the area A_e should not increase during the early development of the cells. For that case, EQUATION 1 shows at once that there should be no systematic difference between cyclonic and anti-cyclonic circulation. Rayleigh's theory deals, however, with a laminar flow pattern, and there has as yet been no evidence that it can be applied to the turbulent processes in the ocean and atmosphere.

The terms "circulation," "cyclonic," and "anti-cyclonic" are usually applied only to motions in horizontal surfaces, but they can be applied just as well to motion in a locally vertical plane (FIGURE 2).* FIGURE



A. Circulation in plane tangent to earth's surface.



Circulation in plane normal to earth's surface.

B. Convection vortex induced by east or west winds.

C. Convection vortex induced by north or south winds.

FIGURE 2. Circulation patterns and their projection on the equatorial plane.

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* FIGURE 2 has been drawn by Mr. W. Von Arx.

2A refers to the usual motion along the earth's surface. Anti-cyclonic circulation in the equatorial plane corresponds to clockwise circulation in the northern hemisphere, counter-clockwise circulation in the southern hemisphere. In each case, the observer is looking down upon the sea surface. The effect of the earth's rotation is proportional to the projection of the area on the equatorial plane, and therefore a maximum at the poles and zero at the equator.

FIGURE 2B shows vertical cells in a meridian plane. This corresponds to the orientation of convection cells resulting from an east or west wind. The projected area upon the equatorial plane is zero, and the Coriolis term disappears from the circulation equation. Therefore,

(1) *East* or *west* winds generate convection cells of minimum or zero asymmetry.

FIGURE 2C shows vertical cells in an east-west plane, resulting from north or south winds. Anti-cyclonic circulation is clockwise in both hemispheres, and the earth's rotation effect is at a maximum at the equator. Therefore,

(2) *North* or *south* winds generate convection cells of maximum asymmetry.

(3) The asymmetry is largest at the equator, smallest at the poles.

(4) The sense of asymmetry depends upon the wind direction, and not upon whether the convection cells are formed in the northern or southern hemisphere.

Conclusion (4) is in disagreement with Woodcock's observations regarding the movement of Portuguese men-of-war in both hemispheres.

(5) To an observer looking down-wind, the *clockwise* vortices should predominate during a *north* wind, the *counter-clockwise* vortices during a *south* wind.

This again disagrees with Woodcock's findings. During 18 measurements in the Gulf of Mexico, the wind had a small southward component, yet the large vortices were predominantly clockwise.

The nature of the asymmetry derived from the circulation theory does not agree at all with the observed pattern. Perhaps the magnitude of the Coriolis force is so small compared to the other forces present that its effect upon the convection cells should be neglected. Assume, as a very rough approximation, a circular convection cell of radius r, and velocity v around the periphery. Actually, the convection cell will not be circular, nor is circular motion required for the application of the circulation theory. However, the assumption of circular motion renders the result in a simpler form without sacrificing the order of magnitude. The angular velocity $\omega = v/r$, and the circulation

$$C = v \cdot 2\pi r = 2\omega A,$$

where A is the area of the cell in its vertical plane. Let θ designate latitude and α the wind direction measured clockwise from the north. The projected area upon the equatorial plane will always be taken as positive, and equals

$$A_e = A \cos \theta \, [\cos \alpha].$$

The circulation theorem (EQUATION 1) can now be written in the form:

$$N = \frac{d}{dt}\left\{ 2A\,(\omega + \Omega \cos \theta \, [\cos \alpha]) \right\}. \tag{3}$$

The importance of the Coriolis term depends upon the ratio

$$\frac{\Omega \cos \theta \, [\cos \alpha]}{\omega}. \tag{4}$$

A very similar ratio appears in Stommel's much more rigorous analysis of the effect of the earth's rotation upon the stability (rather than asymmetry) of convection cells. For a northwest wind in latitude 30°, and for $r = 5$ meters, $v = 2$ cm./sec., the ratio equals about 0.01. The forces required to generate anti-cyclonic circulation are about 2 per cent smaller than for cyclonic circulation. It does not seem likely that such a small difference could account for the asymmetry of the convection cells, and, even if it did, it has been shown that the derived pattern differs in two respects from the observed one.

Perhaps the asymmetry of the convection cells is related to the surface current induced by wind and wave action. This current has a velocity of the order of 2 per cent of the wind velocity, and it is directed approximately 45° from the wind direction, to the right in the northern hemisphere, to the left in the southern hemisphere (FIGURE 3). Adding this surface current vectorially to a symmetrical convection pattern gives a resultant system quite similar to the one observed by Woodcock (FIGURE 1). This explanation is, of course, very incomplete, since it does not even take into account changes of current velocity and direction with depth. It does, however, offer a possible explanation, according to which the asymmetry of the convection cells is brought about not by a direct action of the earth's rotation upon the convective motion, but by the effect of the Coriolis force upon the surface current, which in turn distorts the convection cells into the observed asymmetrical pattern.

Without going further into theoretical considerations, it should be relatively easy to choose between the hypotheses, on the basis of a few critical observations. If the *currents* are responsible, then the asymmetry is independent of wind direction, and changes sign at the equator. If the *direct Coriolis force* is responsible, then the asymmetry

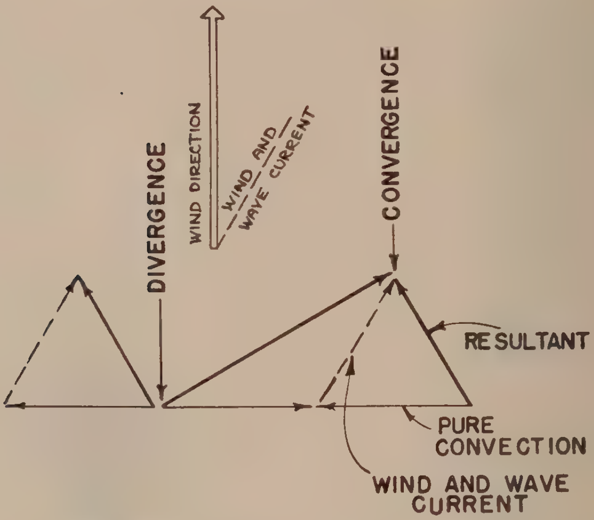

FIGURE 3. Effect of wind and wave current on convection pattern.

should depend upon wind direction, but its sense should be the same in both hemispheres. In this connection, a plot of the asymmetry parameter (EQUATION 4) against observed asymmetry could be useful. From these conclusions, some of the characteristics of the convection cells themselves could be deduced, such as whether and how fast the cells grow, and certain limits regarding the speed of convective movement.

In closing, a brief remark about Stommel's work[2] on the effect of the earth's rotation upon the stability of convection cells may be of interest. His rigorous approach is based upon the development of the Eulerian equations of motion and leads to a partial differential equation of the eighth order. The circulation theory, on the other hand, provides a less rigorous, but more intuitive and much simpler method of attack, which seems particularly well adapted to some of the problems dealing with convection in the atmosphere and ocean.

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THE MAINTENANCE OF INSTABILITY IN THE SURFACE WATERS OF THE OCEAN*

BY JOHN C. ARMSTRONG

Assistant Curator, American Museum of Natural History, New York, N. Y.

INTRODUCTION

During the war, the Navy Oceanographic project at the Scripps Institution of Oceanography had occasion to examine a large number of hydrographic observations from the Kuroshio, south of Japan.

Observations taken during the winter months showed unstable stratification of the surface waters to be a common situation. Before accepting these observations as a basis for naval reports, it appeared desirable to examine such situations, to determine if the known mechanisms of the transfer of heat through a boundary surface could be considered adequate to maintain the recorded instability. The results of this examination form the basis of the present report.

THEORY

Notation

Q_s—radiation absorbed from the sun and sky per unit area and time;
Q_b—the back radiation from the sea surface per unit area and time;
Q_e—the heat used for evaporation per unit area and time;
Q_h—the flux of sensible heat to the atmosphere;
L—latent heat of vaporization of sea water;
C_p—specific heat of sea water;
C_p'—specific heat of air;
ρ—density of sea water;
ρ'—density of air;
ϑ—temperature of the water, C°;
ϑ_w—temperature of the sea surface, C°;
ϑ_a—air temperature at 15 meters above the sea surface, C°;
q_w—specific humidity at the sea surface;

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* Contribution from the Scripps Institution of Oceanography, New Series, No. 313. This work represents results of research carried out for the Hydrographic Office and the Bureau of Ships, Navy Department, under contract with the University of California.

q_a—specific humidity at 15 meters above the sea surface;
U—wind velocity at 15 meters;
γ^2—resistance coefficient when U is measured at 15 meters;
μ_ϑ—coefficient of eddy conductivity of sea water;
μ_s—coefficient of eddy diffusivity of sea water;
S—salinity;
z—depth, taken positive downwards.

We have assumed that the rate of transport of a transferable quantity, such as heat or salinity, by convection or turbulence is proportional to the gradient of that quantity in the direction of transport. It will be convenient to use the term, *eddy conductivity*, for factor of proportionality for the rate of transport of heat, and the term, *eddy diffusivity*, for the rate of transport of salinity. However, it may be noted that it is not intended to make any reservations concerning the mechanism of the convection or turbulence responsible for the transport.

On the basis of such a definition of the eddy conductivity and diffusivity, we may examine the steady-state heat balance when the air is colder than the water.

The Development of Temperature Gradients

FIGURE 1 represents a column of water of unit cross-section, of a height d, and with the upper surface coincident with the sea surface. It is assumed that a current, whose velocity, V, may vary horizontally and with depth, flows through the column from left to right. Then, with $C_p\mu_\vartheta d\vartheta/dz$ as the rate of vertical transport of heat, we may diagram the flow of heat through the column as indicated in the figure.

Therefore:

$$\rho C_p \int_{y_1}^{y_2} \int_0^d V\vartheta dz dy + Q_s + \left(C_p \mu_\vartheta \frac{\partial \vartheta}{\partial z}\right)_d =$$

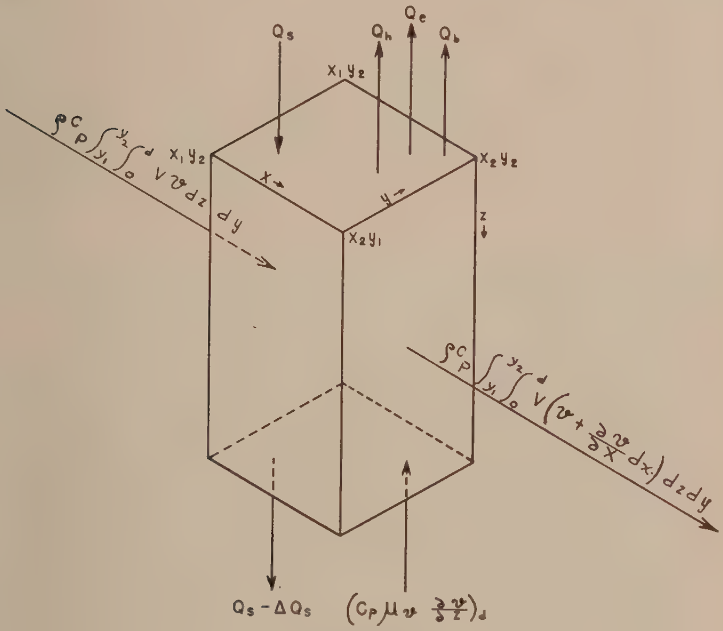
$$\rho C_p \int_{y_1}^{y_2} \int_0^d V\left(\vartheta + \frac{\partial \vartheta}{\partial x} dx\right) dz dy + Q_h + Q_e + Q_s + Q_b - \Delta Q_s. \quad (1)$$

During the winter months in middle latitudes, the combined radiation term $(Q_b - \Delta Q_s)$ is sufficiently small, compared to the other terms, to be neglected in the present discussion. Thus, at about 40° N lat., the average values of Q_b and Q_s from a clear sky are:

$$Q_s = 0.0019;$$
$$Q_b = 0.0030.$$

$Q_b - Q_s = 0.0011$ g.cal./sec., and, as nearly all of Q_s is absorbed in the upper few meters, $Q_b - Q_s$ may be taken as equal to $Q_b - \Delta Q_s$.

The net vertical advection will not be important for small values of d, and by taking the horizontal area sufficiently small, we may neglect the horizontal advection. Therefore, in studying the heat flow of a shallow surface layer, we need not consider the net advection term,



Q_s
Q_h
Q_e
Q_b
$x_1 y_2$
$\rho C_p \int_{y_1}^{y_2} \int_0^d V \vartheta dz$
$x_1 y_2$
x
y
$x_2 y_2$
dy
$x_2 y_1$
z
$\rho C_p \int_{y_1}^{y_2} \int_0^d V(\vartheta + \frac{\partial \vartheta}{\partial x} dx) dz dy$
$Q_s - \Delta Q_s$
$(C_p \mu_\vartheta \frac{\partial \vartheta}{\partial z})_d$

FIGURE 1.

$\rho C_p \int_{y_1}^{y_2} \int_0^d V \frac{\partial \vartheta}{\partial x} dxdzdy$, and may approximate EQUATION 1 by $(C_p\mu_\vartheta d\vartheta/dz)_d = Q_h + Q_e$. Replacing $(\mu_\vartheta d\vartheta/dz)_d$ by $\bar{\mu}\Delta\vartheta/z'$, where $\Delta\vartheta$ is the temperature difference between the surface and a depth z', and where $\bar{\mu}_\vartheta$ is the average eddy conductivity, one obtains

$$\Delta\vartheta = \frac{z'(Q_h + Q_e)}{C_p\bar{\mu}_\vartheta}. \qquad (2)$$

The remaining terms can be written as follows (Burke, 1945; Sverdrup *et al.*, 1942): $Q_h = C_p'\rho'\gamma^2U(\vartheta_w - \vartheta_a)$; $Q_e = L\rho'\gamma^2U(q_w - q_a)$. Then:

$$\Delta\vartheta = \frac{\rho' U\gamma^2 z'[C_p'(\vartheta_w + \vartheta_a) + L(q_w - q_a)]}{C_p\bar{\mu}_\vartheta}. \qquad (3)$$

With the numerical values, $C_p = 1$, $C_p' = 0.245$, $\rho' = 1.25 \times 10^{-3}$ and $L = 585.0$:

$$\Delta\vartheta = \frac{3.06 U \gamma^2 z' [\vartheta_w - \vartheta_a + 2.4(q_w - q_a)]}{\bar{\mu}_\vartheta}, \tag{4}$$

where U is expressed in meters per second, z' in meters, and q in parts per mille.

According to Rossby (1936), when U exceeds 6 meters per second the sea surface behaves as a hydrodynamically rough surface with respect to the wind, and $\gamma^2 = 2.6 \times 10^{-3}$, while for $U < 6$ m./sec., the sea surface behaves as hydrodynamically smooth, and an average value of γ^2 of about 7.4×10^{-4} applies to wind velocities of 2 to 6 m./sec.

The depression of the wet bulb over the Kuroshio (U.S. Dept. Agric., 1940) indicates that the relative humidity of the air is about 80 per cent and, using this value, q_a can be obtained from the air temperature.

Numerical values for EQUATION 4 calculated with the above values and for $z' = 10$ meters may be read from the graph in FIGURE 2.

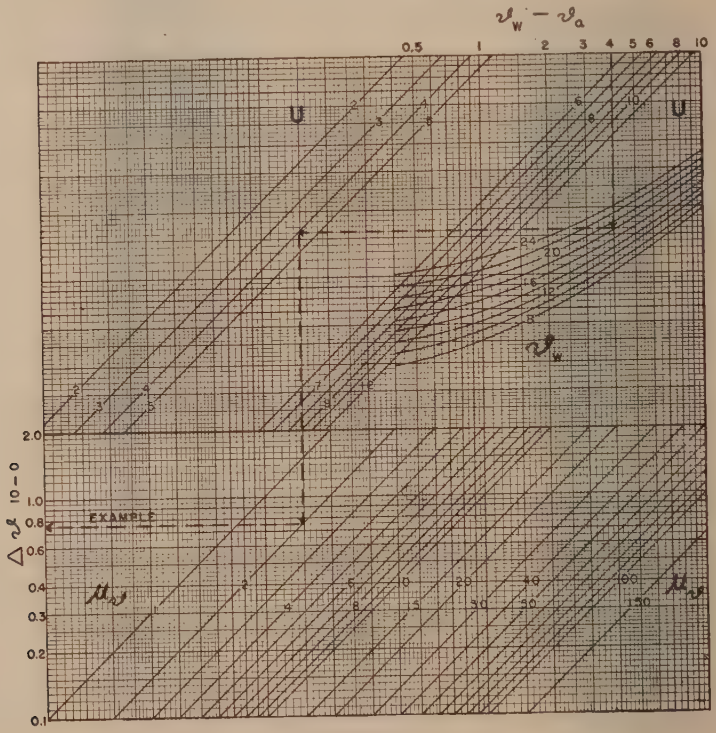


FIGURE 2.

The Development of Salinity Gradients

The salinity gradient may be examined in a similar manner. When a unit mass of water, with a salinity, S, is brought to the surface by turbulence, its salinity is increased by evaporation and becomes $S/1 - E$. With $ds/dt = \mu_s ds/dz$ and E, the evaporation, equal to $\rho'\gamma^2 U(q_w - q_a)$, we obtain:

$$\Delta S = \frac{S_z'\rho'\gamma^2 U(q_a - q_w)}{\bar{\mu}_s}, \tag{5}$$

by reasoning similar to that employed to obtain EQUATION 3.

Numerical values for EQUATION 5 calculated for $z' = 10$ meters, $S = 35.00\%$, and using the same values of ρ' and γ^2 as in EQUATION 4, may be read from FIGURE 2.

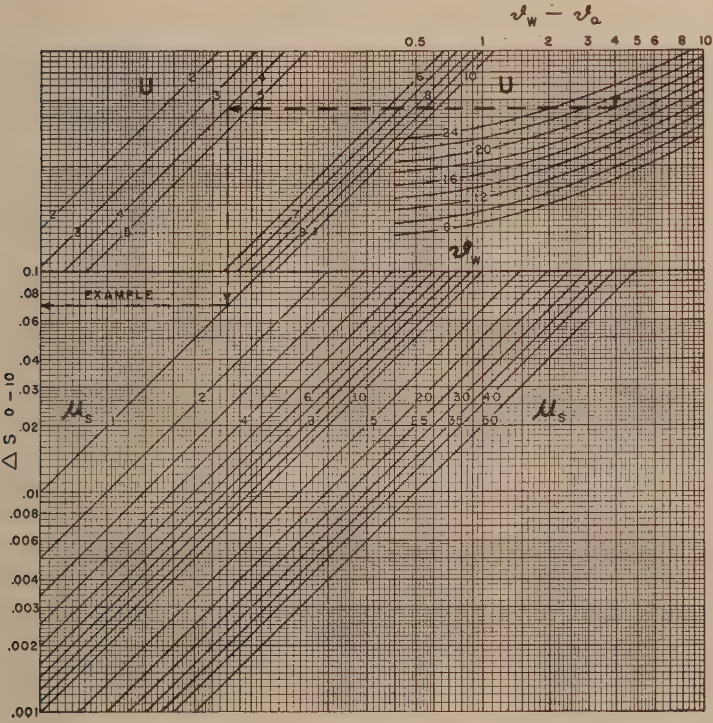


FIGURE 3.

Explanation of FIGURES *2 and 3*

Both diagrams are used in a similar way, and the manner in which this is done may be illustrated by the following example, which has been entered upon FIGURE 2 in broken lines:

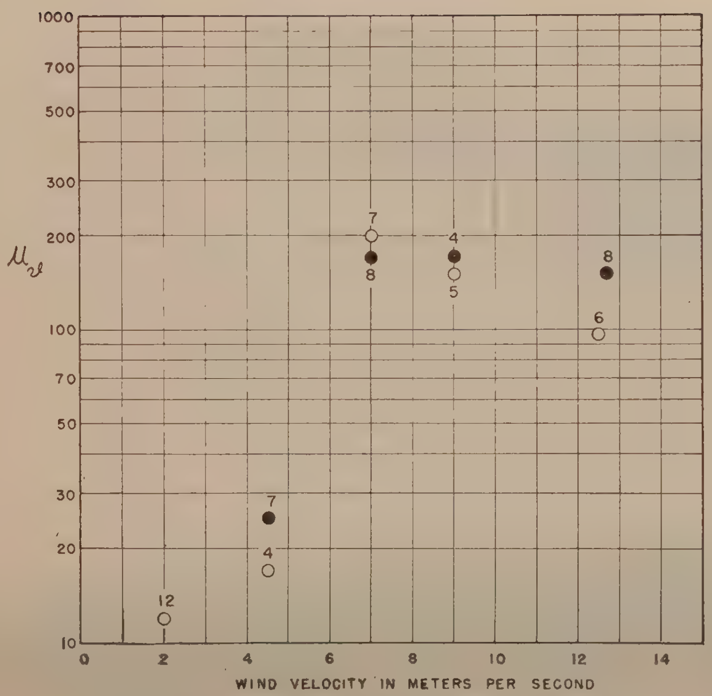


FIGURE 4. Values of the eddy conductivity computed from the *Mansu* data.

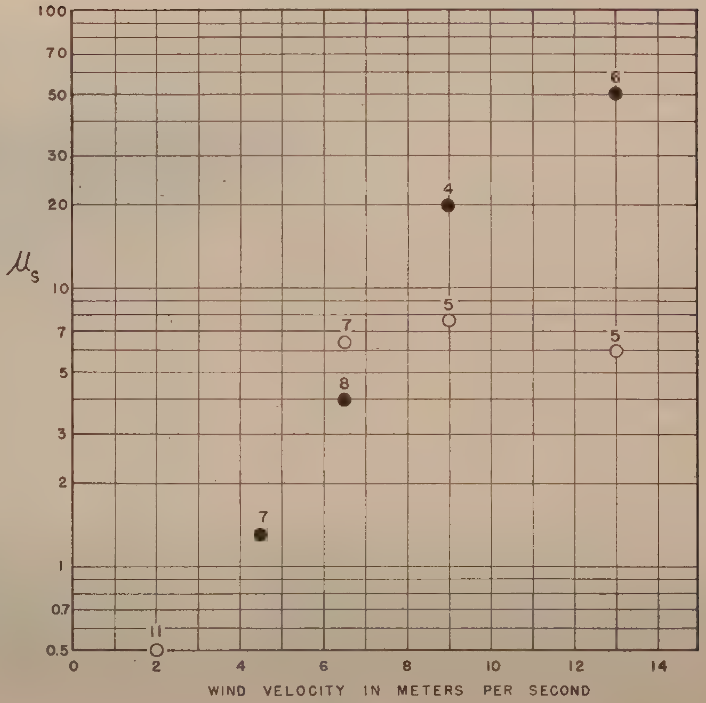


FIGURE 5. Values of the eddy diffusivity computed from the *Mansu* data.

Figures over points indicate number of observations. ○ = November data; ● = January-March data.

Given: $\vartheta_w - \vartheta_a = 4°$, $\vartheta_w = 20°$, $U = 4$ m./sec.,

$\bar{\mu}_\vartheta = 20$ g. cal./cm.^{2}/sec., $z' = 20$ meters; find $\Delta\vartheta_{20-0}$.

(1) Enter FIGURE 1 with $\vartheta_w - \vartheta_a = 4°$ at the top right-hand scale and read down to $\vartheta_w = 20°$.

(2) From the point found in (1), read across to $U = 4$.

(3) From the point found in (2), read down to $\mu_\vartheta = 2$.

(4) From the point found in (3), read across to the scale and find 0.75°. As moving the decimal point over 1 place to the left in μ requires shifting the point 1 place to the right in $\Delta\vartheta$, $\Delta\vartheta_{10-0} = 0.075°$, $\Delta\vartheta_{20-0} = 0.15°$ C.

Answered.

Comparison of Theory with Hydrographic Data

The most readily available data, which include the air temperature and the velocity of the wind, are those obtained by the Mansu in the Kuroshio during the winters of 1925 to 1928 (Imperial Japanese Navy, 1933). After the elimination of stations located in areas where there was danger of contamination by run-off water, there were available 39 observations made in November, 1925, and 28 made at various times in January, February, and March from 1926 to 1928.

The data were averaged by classes corresponding to wind velocities of 1-3, 4-5, 6-7, 8-10 and 11-15 meters per second, z' as the depth to the deepest observation showing a temperature increase, and the values of μ_ϑ and μ_s computed by means of EQUATIONS 4 and 5. The results are shown in FIGURES 4 and 5. The values obtained for μ_ϑ are in general agreement with the range 12-135 published by Suda (1936). Suda's values were derived from a consideration of the annual march of temperature at various levels, and thus represent the average over the entire year. They are not, therefore, strictly comparable to values obtained from EQUATIONS 4 and 5.

The somewhat unexpected result that $\mu_\vartheta > \mu_s$ may be further examined in data for which the wind velocity is lacking, by making use of the relation $\frac{\mu_\vartheta}{\mu_s} = 7.0 \frac{\vartheta_w - \vartheta_a}{q_a - q_w} + 16.1 \frac{\Delta S}{\Delta\vartheta}$, derived from EQUATIONS 4 and 5. The best data available for this purpose are from four sections run across the Kuroshio during the winters of 1929, 1930, and 1937 (Tokyo Imperial Fisheries Station). As may be seen in TABLE 1, $\frac{\mu_\vartheta}{\mu_s} > 1$ in each case.

TABLE 1

DATA FROM SECTIONS RUNNING S SE OFF ASHIZURISAKI

The station closest to land has been omitted in each case. The data from all other stations have been averaged for each section.

Section	No. of obs.	ϑ_a	ϑ_w	z'	$\Delta\vartheta$	ΔS	$\frac{\mu_\vartheta}{\mu_s}$
Jan. 14–15, 1929	10	6.2	19.9	21.5	0.24	0.13	4.3
Feb. 7–8, 1930	10	6.0	19.4	15.0	0.18	0.24	30.0
Dec. 7, 1930	8	17.4	22.1	10.5	0.12	0.09	2.2
Feb. 3–4, 1937	14	13.7	20.0	10.3	0.10	0.06	12.0

Discussion

It was concluded that the recorded instability was of an order of magnitude that could indeed be maintained by the cooling of the surface water. The observations were, therefore, included in the studies made for the Navy.

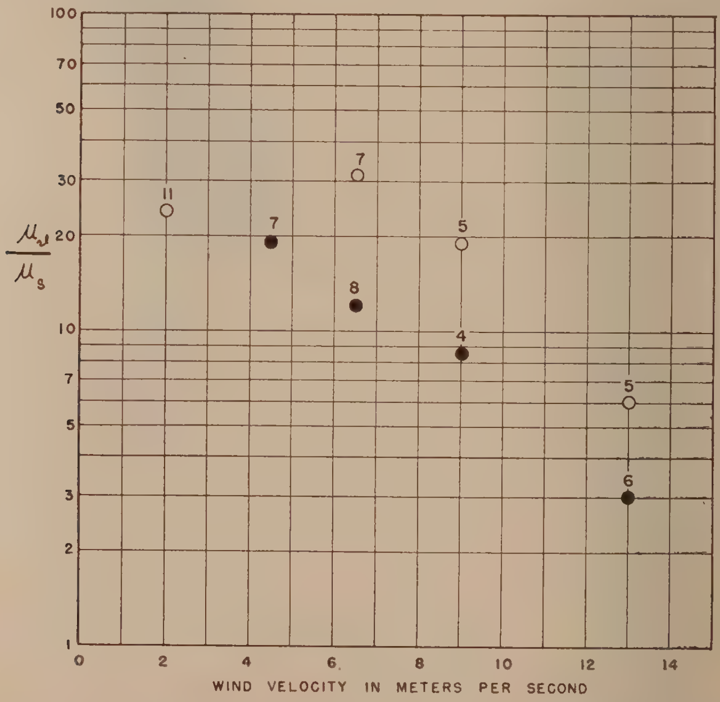


FIGURE 6. Values for the ratio $\frac{\mu_\vartheta}{\mu_s}$ computed from the *Mansu* data. Figures over points indicate number of observations. ○ = November data; ● = January-March data.

Perhaps the most interesting result is that $\mu_\vartheta > \mu_s$. It may be noted that the ratio of the rate of molecular conductivity is very nearly 70 times the molecular diffusivity in sea water. In FIGURE 6, it may be seen that the ratio appears to approach this value at zero wind velocity, and that μ_ϑ may equal μ_s at very large wind velocities. While our studies have not so far indicated the nature of the mechanisms, this would seem to suggest that the change in the ratio $\frac{\mu_\vartheta}{\mu_s}$ may be related to the physical size and mean velocity of elements of water involved in the turbulent process.

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DISCUSSION OF THE PAPER

Dr. R. B. Montgomery (*Woods Hole Oceanographic Institution, Woods Hole, Massachusetts*):

In order to estimate the degree of instability that may exist below the sea surface, Mr. Armstrong has made certain assumptions, without emphasizing the uncertainty that they introduce. The greatest uncertainty appears to lie in the assumption of constant temperature gradient and constant eddy conductivity from the sea surface down to depths as great as 20 meters. In contrast, the conductivity presumably has the molecular value at the sea surface and increases with depth by several powers of ten. The temperature gradient, correspondingly, is very large next to the surface and is very small even at a depth of only one meter, as was indicated in my schematic illustrations.* However, since the so-called *sur-*

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* **Montgomery, R. B.** Introduction: problems concerning convective layers. Ann. N. Y. Acad. Sci. **48**(8): 707–714.

face water temperatures were undoubtedly measured at a depth of about a meter rather than at the surface, this assumption is probably not so serious as to affect the order of magnitude of the results obtained.

Another assumption is involved in the use of Burke's formula to compute the heat transfer to the air. In deriving his formula, Burke has assumed, without any discussion, that the transfer of heat is identically similar to the transfer of momentum. As I have had occasion to point out previously, it does not appear possible that heat and momentum are similarly transferred through the laminar boundary layer. Support for Burke's formula is to be found in the marked success he attained in estimates of air temperature, and in the observations of temperature gradients above the sea surface recently published by Dr. Sverdrup. Even though the formula may be based on an erroneous assumption, it therefore appears to be approximately correct.

Although the approximations that Mr. Armstrong has had to make prevent his results from having great accuracy, I do not see that the order of magnitude should be affected. I should like to point out that his estimate of the degree of instability that can occur in the ocean is of interest and value, especially because it appears to be the first that has been attempted.

Contribution No. 314

Contributions from the Scripps
Institution of Oceanography
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Apparatus for Rapid Conductometric Titrations

Determination of Sulfate

LLOYD J. ANDERSON[1] AND ROGER R. REVELLE[2], *Scripps Institution of Oceanography, La Jolla, Calif.*

This paper describes the development and construction of electrical apparatus suitable for conductometric titrations, and presents a method of using the apparatus for macro- and microdeterminations of sulfate. When the precipitation is controlled by seeding, amounts of sulfate as small as 1 mg. can be determined to ±1% even in the presence of more than fifty times as much chloride.

MEROUS attempts have been made to develop simple and pid procedures for determining dissolved sulfate. Simple ct titration procedures with barium solutions have been le because of the lack of reliable color-changing end-point rs. As a result, a great many indirect methods have vised in which the unknown sulfate is precipitated by a reagent and an equivalent amount of some other ion, determine, is liberated. The methods of Muller (*7*), (*3*), and Webb (*12*), though usually less time-consuming conventional gravimetric procedure, leave something to ed in the way of reliability and accuracy. One color r for direct barium titration has been used by Robertson bb (*9*), who state, however, that "the simplicity of the is to some extent outweighed by the capricious behavior dicator".

al electrometric methods have been developed in which point is recognized by the aid of potentiometric or contric indicators. Reversible sulfate electrodes are not for routine work because they require extreme care, in nstruction and use, in order to prevent "oxygen poisoning". Bimetallic electrodes (*13*) are often suitable for pure solutions but become insensitive in mixtures. Dutoit (*2*) was the first to apply the conductometric titration technique to sulfate determination and numerous others have reported using the method. Kolthoff and Kameda (*5*) investigated the reliability of the conductometric titration for sulfate and concluded that the procedure is too inaccurate for most analytical work, but that coprecipitation of sulfate, the usual nemesis of sulfate determinations, does not occur and hence cannot account for their low results. They also found that the mere presence of the barium sulfate precipitate greatly affected the conductance changes measured during the titration.

In the present method, the precipitation is seeded with a small amount of pure barium sulfate. The seed crystals were precipitated from a solution of C.P. barium hydroxide by adding a slight excess of C.P. sulfuric acid and allowing the washed precipitate to stand for several weeks. These factors tended to produce comparatively large seed crystals. With such crystals as precipitation nuclei the effects of adsorption should be minimized.

One would also expect seeding to produce precipitates that were much more uniform from one titration to the next. Perhaps the more uniform results reported herein are due in large part to

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t address, U. S. Navy Electronics Laboratory, San Diego, Calif.
t address, U. S. Navy Bureau of Ships, Washington, D. C.

seeding the titration mixtures. From the standpoint of convenience, the greatest advantage in seeding lies in accelerating the precipitation rate and thus reducing the titration time from 30 to 5 minutes per sample.

The chief limitation to conductometric titration of sulfate lies in the concentrations of anions other than sulfate in the solution. When these are large, it is necessary to use a concentrated barium solution and microburet for titration in order to maintain a well-defined "break" in the titration curve of meter reading versus volume of reagent added. In the present method, the breaks in the curves were sufficiently well defined to obtain an accuracy of ±1% even in solutions where the ratio of chloride to sulfate was as high as 56 to 1.

APPARATUS

The electrical circuit can be divided into three more or less distinct units: source of alternating current, Wheatstone bridge, and vacuum tube voltmeter.

The alternating current source is a conventional type of resistance-tuned oscillator driving a 6F6 power tube, and supplies 20 volts of 1000-cycle alternating current to a 500-ohm bridge. An inductance-type oscillator is avoided to reduce induction of spurious currents in the bridge. In the circuit diagram (Figure 1) the oscillator and its power pack are shown at the top. The output of the power pack is stabilized against line voltage changes by gas-discharge voltage-regulator tubes. These are commonly used for such purposes and in this case have proved very
in keeping the power delivered to the bridge constan
narrow limits.

In order to prevent direct contact between oscilla
bridge, the alternating current is supplied through an im
matching output transformer. It was felt desirable to m
oscillator and power pack on a chassis separate from the re
circuit in order to reduce further the possibility of induc
dom voltages into the bridge, and to decrease the am
equipment needed on the titration bench itself. The
fed from the oscillator to the bridge through a flexib
fitted with jacks for convenience in disconnecting the t
when desired. The bridge is a continuous deflection typ
than the conventional slide-wire and null indicator. Thi
bridge requires no manipulation during a titration, si
ductance changes are read directly from the meter.

Such operation eliminates the necessity of a calibra
cision slide-wire and aids greatly in reducing the size
pense of the apparatus. In this case a simple carbon-
volume control was found to be perfectly satisfactory
variable arm of the bridge. This unit, R_{15}, is compact
to allow it and the other components of the bridge circui
the conductance cells themselves, to be mounted inside th
containing the voltmeter. Thus all the electrical con
quiring adjustment during a series of titrations are locate
panel on the front of the compact bridge voltmeter unit.

In the circuit diagram, two conductance cells are in
Titrations are carried out in only one of them. The fu
the other is merely to balance out incidental conductance
due to temperature drift and any other changes not dire
nected with the titration itself. Theoretically, comple
pensation will result only if both cells have the same vol
conductance, since only under these co
would the temperature rise be identical
cells. Fortunately this condition can b
attained: First, the variable bridge resis
is set at its electrical center and the dial is
for future settings. Then one cell is fil
the solution to be titrated and the seco
filled with a slightly smaller volume of a
solution. Now, concentrated sodium ch
distilled water is added until the voltme
cates that the bridge has reached balanc

If a series of titrations is to be made
tions of nearly the same conductivity, it
be necessary to readjust the resistance of
trol cell each time. Practice indicates t
ferences even as high as 25% do not ca
serious drifting of the bridge balance. I
however, to start a series with the cond
nearly equal.

The vacuum tube voltmeter, used here
cate conductance changes, is shown sche
at the lower right of Figure 1. It is a
type of capacity-coupled voltmeter,
numerous features adapting it to the
purpose.

Most important of these, from the sta
of convenience and increased sensitivit
so-called "D-battery" circuit compose
S_2, and R_{22}. The function of this circ
by-pass most of the plate current of t
tube but to allow the fluctuations to go
undiminished through the meter. This
ment permits the use of a more sensitiv
thereby increasing the effective sensitivi
instrument. Actually, this device is n
nor even a recent development. Kin
Garman (*4*), Morton (*6*), and others (*8*,
reported using it in electrochemical inst
and its use is also commonplace in purel
cal apparatus. In the present circuit, t
the D-battery increased the effective se
of the voltmeter eightfold.

A further advantage of the D-battery
ductance voltmeter is that it affords an i
ent control for placing the meter needl
desired point on the scale. This is par
useful in spacing a series of titration c
a plotting sheet.

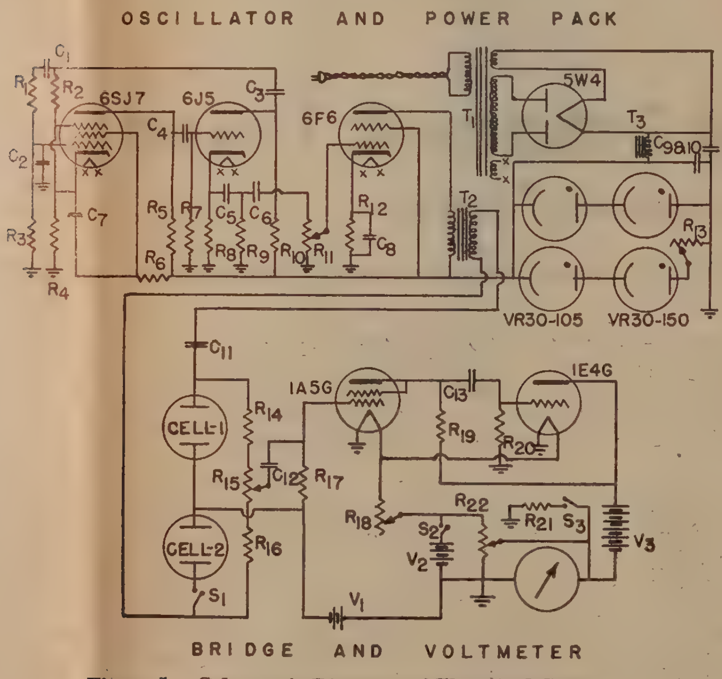
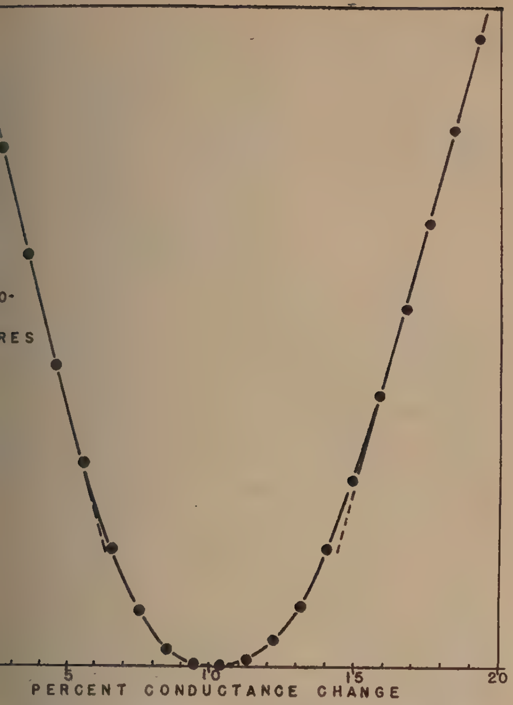


Figure 1. Schematic Diagram of Electrical Circuit

R_1.	15,000 ohms
R_2.	2,000 ohms
R_3.	10,000 ohms
R_4.	Two 6-watt 120-volt lamps in series (ca. 1000 ohms)
R_5.	100,000 ohms
R_6.	500,000 ohms
R_7.	500,000 ohms
R_8.	1,000 ohms
R_9.	5,000 ohms
R_{10}.	20,000 ohms
R_{11}.	500,000 ohms
R_{12}.	660 ohms
R_{13}.	500 ohms
R_{14}, R_{16}.	100 ohms
R_{15}.	1,000 ohms
R_{17}.	3,000,000 ohms
R_{18}.	25 ohms
R_{19}.	500,000 ohms
R_{20}.	250,000 ohms
R_{21}.	10 ohms
R_{22}.	10,000 ohms

C_1,C_5.	0.01 mfd. 600 volt
C_3.	1.0 mfd. 600 volt
C_4,C_7.	0.5 mfd. 600 volt
C_2,C_8.	10.0 mfd. 25 volt electrolytic
C_6.	0.01 mfd. 600 volt electrolytic
C_9,C_{10}.	8.0 mfd. 600 volt electrolytic
C_{11}.	0.20 mfd. 600 volt electrolytic
C_{12}.	0.10 mfd. 600 volt electrolytic
C_{13}.	0.02 mfd. 600 volt electrolytic
V_1.	Two flashlight cells in series
V_2.	Two heavy duty 1.5-volt cells in series
V_3.	Two heavy duty 45-volt cells in series
T_1.	120 volt primary, 5.3 volt, 6.3 volt, and 660 volt c.t. secondary
T_2.	7000-ohm primary, 500-ohm secondary

Microammeter, 0–500 microamperes, 130-ohm coil; Triplett Model 521



2. Over-all Sensitivity Curve of Electrical Circuit

nably the voltmeter sensitivity could be further increased
; more stages of amplification. The practical limit of
rocedure is the point where random fluctuations begin to
on the meter. The sensitivity of the present voltmeter is
t this limit. Meter fluctuations occur, for example, if
ng of the cells is not sufficiently smooth or if large bubbles
f precipitate approach the electrode surfaces too closely.
sonable care, however, the meter action is smooth and
The actual sensitivity is about 2500 microamperes per
vith the meter selected, about 600 mm. per volt.

2 shows the over-all response of the instrument to
in conductivity in one of the cells. It is seen that the
is linear until the readings are within 150 microamperes
ll point. Inside this limit the sensitivity falls rapidly,
; zero at balance, then rising again as the balance point
. The reason for this behavior lies in the voltmeter it-
e microammeter responds to differences in the slopes of
segments of the S-shaped characteristic grid voltage–
rent curve. As the input voltage from the bridge is re-
ar balance, these adjacent segments encompass a smaller
ller total portion of the curve and hence the difference
slopes approaches zero and the voltmeter becomes more
e insensitive. The response of the voltmeter could un-
y be made virtually linear if it were necessary, but in
the restriction imposed offers no serious disadvantage
ctometric titration work.

ual practice, the electrical circuit as described above is
sfactory. As in most other vacuum tube instruments, a
mount of drift in meter readings is noted just after the
s is turned on. With fresh batteries, this amounts to
microamperes per minute at first and after 15 minutes is
nth of this.

drift amounts to only 2 or 3 microamperes for an entire
while the total change to be measured is of the order of
00 microamperes. As the plate batteries age, the drift
. For example, after 6 months of normal battery use
it 80 microamperes per minute initially and drops to 2
peres per minute after half an hour. Even this latter
ot troublesome, since it is uniform for a given titration and amounts to only a small percentage of the total change to be measured.

Furthermore, although it is not a novel one, the two-cell method of compensating for temperature and other incidental effects has proved effective with present apparatus. When the cell conductances are properly equalized and the apparatus is set in operation, the meter readings remain constant, except for the small voltmeter drift. When changes of conductance are set up in one of the cells, the meter responds at the rate of 9-mm. deflection for each 1% conductance change. This makes possible the detection of changes of about 0.02%.

The conductance cells constitute the remainder of the electrical equipment.

Two sizes were used: a pair of 500-ml. cells for large samples and a 100-ml. pair for micro work. They were made from ordinary reagent bottles and each cell had a pair of pure silver electrodes sealed on opposite sides of the cell near the bottom. In the 100-ml. pair the electrodes were 6 mm. in diameter and in the 500-ml. pair were 18 mm. in diameter. These dimensions were found optimum to obtain maximum oscillator output and without undue polarization difficulties. The electrodes were sealed in the cell with De Khotinsky cement and connecting wires were brought out through small holes drilled through the cell wall.

One pair of cells was made using platimum electrodes instead of silver. It was found that, on passing 60-cycle current through these cells, gas bubbles appeared on the surface of the platinum when only a few volts were applied, whereas with silver electrodes 20 volts could be applied with no gas liberation or conductance instability of any kind. Although the frequency was subsequently raised to 1000 cycles, silver electrodes were still favored because of their reduced tendency to cause electrolysis of the solutions.

The only other part of the apparatus needing special mention is the microburet, which was made according to a description by Scholander *(10)* and has proved very precise and reliable. In principle, the buret operates by the displacement of mercury from a reservoir by the spindle of a micrometer caliper. This, in turn displaces the reagent from the buret into the titration cell. When calibrated for irregularities in the diameter of the spindle, the buret was found to deliver to ±0.0003 ml. It has a total volume of about 0.69 ml.

TITRATION PROCEDURE

With S_1 open and S_3 closed, the oscillator and voltmeter are set in operation by plugging the oscillator cord into a 60-cycle 115-volt outlet and closing S_2 on the voltmeter chassis.

Next, the sample to be titrated is introduced into the cell and diluted to a convenient level. The conductance of the control cell is adjusted roughly to that of the titration cell by filling it with nearly the same volume of a similar solution. Switch S_1 is closed, allowing current to flow through the cells, and then the knob on R_{22} is rotated slowly to the right until the meter reading reaches a maximum and decreases to about 30 microamperes. Now the meter is thrown on high sensitivity by opening S_3. The null point is located on the meter by adjusting the bridge knob, R_{15}, until the point of maximum reading is found. Next, with the bridge set at its electrical center, a small amount of water or concentrated salt solution is added until the null point is just reached by the meter. This will bring the two conductances very nearly to equality and requires but little time to perform. If the cells were made nearly identical, the volumes of solution in the two should also be the same, ensuring effective compensation of all incidental drifts occurring in the cells.

By now the electrical circuits will have settled down to a steady state and the titration can be started. A small amount of reagent is added to the sample in order to determine the direction in which the meter will deflect during the titration. The bridge knob should be set on the side of balance giving a needle deflection away from the null point. In order to keep the meter readings on the range of linear response, the bridge is adjusted so that the needle is about 150 microamperes away from the null point at the start of the titration.

It is usually sufficient to plot only about five points before the end point and an equal number after. Figure 3 shows a series of check runs made on sea water, representative of the straight lines

Table I. Sulfate Analyses on 25-Ml. Samples of Sea Water

Bottle No.	0.208 M $Ba(NO_3)_2$ 1st	2nd	3rd	4th	Average	Sulfate	Chloride	$\frac{SO_4^{--}}{Cl^-}$	Probable Error
	Ml.	*Ml.*	*Ml.*	*Ml.*	*Ml.*	*Mg.*	*Mg.*		
1	3.270	3.251	3.281	...	3.267	65.50	469.0	0.1397	±0.0005
2	3.279	3.287	3.304	3.320	3.297	66.10	475.5	0.1391	±0.0007
3	3.377	3.370	3.352	3.328	3.357	67.30	480.5	0.1400	±0.0008
4	3.282	3.311	3.299	3.288	3.295	66.06	472.5	0.1398	±0.0005
5	3.282	3.270	3.287	3.304	3.286	65.88	471.5	0.1397	±0.0005
						Average ratio		0.1396	±0.0006

formed by the experimental points. The dotted lines represent theoretical slopes and the theoretical end-point level.

EXPERIMENTAL RESULTS

Macromethod. Table I shows the results of sulfate analyses carried out on a series of samples of sea water obtained off the coast of Southern California. The average weight ratio of sulfate to chloride found for all the samples was 0.1396 ±0.0006. This agrees well with 0.1394, the accepted ratio for the major oceans of the world (*11*).

The work on sea water showed that calcium interferes seriously with conductometric determinations of sulfate. Analytical results come out about 5% low in sea water, for example, because of its presence. Fortunately, the effect of calcium can be neutralized by adding sodium oxalate before titrating, provided the ratio of sulfate to calcium is at least 6 to 1.

The effect of oxalate appears to be due to mass action equilibria. One may consider that a competition exists between barium and calcium for the sulfate, which results in partial substitution of calcium for barium in the barium sulfate crystals. Such behavior becomes the more likely because of the chemical similarity of barium and calcium as well as the isomorphism of their sulfates.

When oxalate is added, another competition is set up between calcium and barium for the oxalate, resulting in coprecipitation of barium with the calcium oxalate. When the ratio of oxalate to calcium is about right, the amount of sulfate used up by the calcium is equal to the barium used up by the oxalate, and the results come out equal to theoretical. For sea water the optimum ratio of calcium to oxalate is empirically found to be about 3–6 to 1. If much more oxalate than this is used, the results are too high, while if much less is added, they are too low. When the calcium-sulfate ratio is greater than 1 to 6, titration end points become erratic and oxalate seems to be ineffective.

Owing to the low initial concentration of sulfate in the titration mixtures (0.0015 M), it was found advantageous to seed the precipitation with a little pure barium sulfate. The time required to make a titration without seeding is about 30 minutes but is reduced to about 5 minutes in a seeded mixture. Seeding also seems to be responsible for minimizing coprecipitation effects and for producing precipitates of more uniform character.

The seed is prepared by adding C.P. sulfuric acid to C.P. barium hydroxide until the mixture is acidic. The precipitate is then washed on a sintered-glass filter with 3% acetic acid until no cloudiness is observed on mixing a little of the clear filtrate with concentrated barium solution. The product is stored in 3% acetic acid in order to prevent the absorption of carbon dioxide and the subsequent formation of barium carbonate. The addition of a small amount of acetic acid is necessary in sea water titrations, in order to prevent precipitation of barium by the carbonate and bicarbonate present in the sea water. The presence of a small amount of acetic acid should have no deleterious effect upon most other types of sulfate titrations, while its presence in the seed suspension ensures its remaining pure on standing. When the suspension is made just thin enough to be easily pipetted, about 5 ml. are sufficient for 500 ml. of titration mixture.

The accuracy and precision of the method were checked using artificial sea water, both with and without calcium and with a known concentration of sulfate.

In the artificial sea water mixture, the required weight of Baker's C.P. sodium sulfate was dried for 72 hours at 110° C. and weighed into the volume
containing sodium, magnesium
cium chlorides.

Before addition of the sul
dilution to volume, the chlor
tested for sulfate by adding con
barium nitrate to a sample of
centrated chloride solution.
of cloudiness was observed.
mg. of sulfate was added to th
a decided cloudiness appeared, i
that previously the salts were su
sulfate-free for the purpose. T
nitrate solution was made up wit
C.P. barium nitrate which had been dried for 72 hours a

Both solutions were standardized gravimetrically by
slight excess of sulfate or barium, respectively, to known
of the solutions to be standardized. The precipitation w
out by adding one reagent dropwise to a hot solution of
and digesting the precipitate for 2 hours on a steam b
initial concentration of the unknown ion was appr
0.015 M. Enough hydrochloric acid was added to th
to make it 0.3 M in hydrochloric acid. These condit
found by Crowell (*1*) to be optimum for avoiding abs
nitrate by the barium sulfate precipitate. Two run
standard barium solution agreed to 0.15% and two ru
artificial sea water agreed to 0.12%.

A secondary method for standardizing the barium nit
tion also gave good agreement. This method involved
ing a known volume of the solution to dryness on a st
and heating at 140° C. for 72 hours. Two runs by th
checked to 0.1%, but the value arrived at was 0.3% hi
that given by the precipitation method. Owing to
bility of occluded water in the barium nitrate crystals
cipitation results were favored.

Numerous conductometric runs were made on the
sea water to determine the per cent recovery and the
error of individual titrations. Next, the sulfate conte
creased and further runs were made (Table II). In
containing calcium, sodium oxalate equivalent to $^1/_5$ of

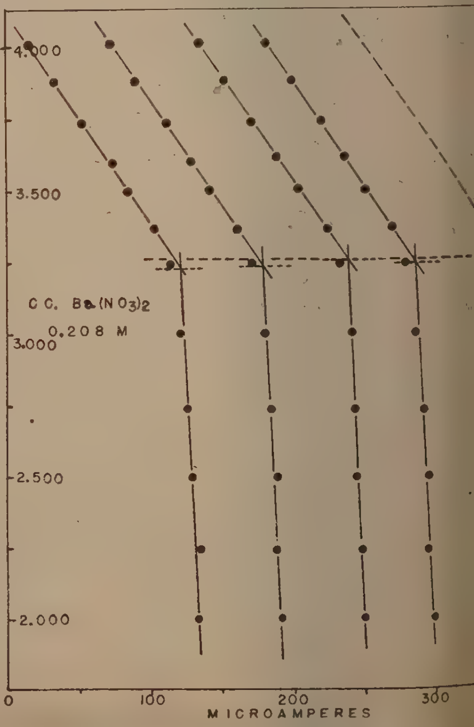


Figure 3. Plot of Typical Titration Dat

Total sulfate approximately 65 mg.

present was added before each
he data indicate an average of
recovery of the total sulfate
nd an average probable error of
.
method. All the previous ti-
were made with 500-ml. cells
ml. buret for the barium nitrate.
to adapt the method to mi-
minations, it was necessary to
oth sizes.
r of 100-ml. cells was made
o the larger ones, and the mi-
mentioned above was also constructed.
investigation of the suitability of the method for micro
sulfate solutions were merely mixtures of sodium sulfate
um chloride in varying proportions. Since sea water
s were as successful as those of simpler mixtures in the
ork, it was tacitly assumed that the sulfate-chloride mix-
uld afford as good a test of the method as more complex
.
III shows the results obtained from the investigation and
the suitability of conductometric titrations for sulfate
micro analyses. It is seen, for example, that 1 mg. of sulfate can be determined to ±1% even in the presence of 56 times as much chloride.

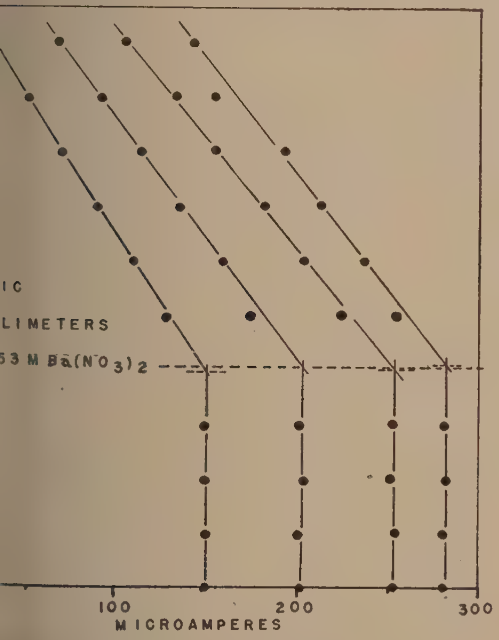


Figure 4. Plot of Sulfate Microtitrations

Total sulfate approximately 1 mg.

. Sulfate Determination on Artificial Sea Water

Water, lcium- Free	Sea Water with Calcium and Oxalate	Sea Water, Calcium-Free with Added Sulfate
	Mg. of Sulfate Added	
7.05	68.00	134.67
Mg. of Sulfate Recovered in Individual Titrations		
7.08	67.32	134.28
6.40	67.97	134.34
6.76	67.86	133 92
7.26	68.20	134.30
6 64	68.07	134.12
7.10	...	134.12
7.00	...	....
6.82	...	....
% Recovery and Probable Error of Individual Titrations		
5 ±0.39	99.82 ±0.45	99.64 ±0.11

Table III. Microdeterminations of Sulfate

$\frac{Cl^-}{SO_4^{--}}$	SO_4 Added	Sulfate Found in Titrations						Recovery and Probable Error
		1st	2nd	3rd	4th	5th	Average	
	Mg.	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*	%
1.25	16.00	16.07	16.03	15.60	15.67	...	15.84	99.0 ±1.3
3.75	16.00	15.72	15.92	15.90	15.90	15.78	15.84	99.0 ±0.5
3.75	16.00	15.42	15.70	15.70	15.58	...	15.60	97.5 ±0.7
5.00	12.00	11.81	11.83	11.97	12.07	11.91	11.92	99.4 ±0.8
5.00	12.00	11.95	11.85	11.95	11.95	11.92	11.92	99.4 ±0.3
15.00	4.00	4.02	4.09	4.02	4.03	4.01	4.03	100.8 ±0.7
56.25	1.067	1.064	1.067	1.040	1.070	...	1.060	99.3 ±1.1
56.25	1.067	1.078	1.075	1.056	....	...	1.070	99.7 ±0.9

In Figure 4 are plotted the titrations tabulated on line 7 of Table III. The experimental points in this case form just as good straight lines as those in Figure 3, where about sixty times as much sulfate was present. With still smaller cells and more refined technique, there is no reason why accurate determinations on considerably smaller amounts of sulfate could not be carried out.

The apparatus described in this paper has also been used in chloride titrations with considerable success. Results will be presented in a subsequent paper. Comparison indicates that the conductometric method of recognizing the chloride–silver nitrate end point is capable of precision and accuracy fully comparable to those of precise chemical methods.

SUMMARY

The method, with suitable apparatus for determining amounts of dissolved sulfate as small as 1 mg. with an accuracy of ±1.0% even in the presence of considerable chloride, is a modification of the familiar conductometric titration. It deviates from the classical method in that the apparatus registers conductance changes automatically. Temperature drift in the conductance cell is compensated without the necessity of a thermostatic bath.

Calcium interferes with the determination, but its effect can be eliminated by use of oxalate, provided the ratio of sulfate to calcium is at least 6 to 1. The time required for a titration can be shortened from 30 to 5 minutes by the addition of a small amount of pure barium sulfate.

In macrodeterminations, when the precipitation was controlled by seeding, recovery averaged 99.74% of the total sulfate present, with a probable error of ±0.32%. In micro amounts (1 to 16 mg.) recovery averaged 99.3% and the probable error was ±0.8%. These results show less probable error than is usual in conductometric sulfate determinations. This uniformity is probably due to the presence of more uniform precipitates, which in turn were produced by providing seed crystals on which the precipitation could take place.

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Contribution No. 315

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ABUNDANCE OF DESERT ANIMALS INDICATED BY CAPTURE IN FRESH ROAD TAR[1]

The apparent paucity of animal life in the desert is misleading. Under appropriate conditions great numbers of cryptic animals come into sight. Thus at night, after a torrential rain in September, 1926, one of us saw, at Fort Yuma, California, unbelievable numbers of toads and insects about lights. In general, under such conditions, the animal life tends to keep pace with the sudden flourishing of the plant life. Even under ordinary xeric conditions supposedly rare animals may be seen in considerable numbers by a trained observer at night, for instance by a herpetologist following the new technique of slowly driving on paved roads (Klauber, '39). Or one may find in its special retreat large numbers of a species that shuns the heat and light of the desert day. Some of these and other methods of collecting may provide a rough quantitative estimate of the abundance of certain species, but will not give a satisfactory estimate of the abundance of desert life as a whole.

One method of expressing the real abundance of desert animals is suggested by some observations that we made in the Mohave Desert in southeastern California on June 26, 1946. Here we found large numbers of animals trapped in fresh tar that had been laid during the night along half of the paved county road that parallels the Los Angeles Aqueduct from Parker (Arizona) westward, near the southern border of eastern San Bernardino County. After turning southwest on this road from Vidal Junction on U. S. Highway 95 we noticed that during the previous night lizards and rodents had become trapped in the fresh tar. After travelling the county road for 4.9 miles it became evident that a collection of the entrapped animals might be profitable.

Between 6:00 and 7:00 A.M. a two-quart jar of specimens was filled with trapped animals from 2.3 miles of road. During the next hour (7:00 to 8:00 A.M.) a second jar was filled along the following 3.5 miles of road (on either side of the railroad station named Grommet). The animals collected are tallied in table I. The identifications were kindly supplied by staff members of the San Diego Museum of Natural History: the arthropods by Charles F. Harbison; the reptiles by Laurence M. Klauber, and the mammals by Laurence M. Huey. The specimens, in part, are kept in that museum. It was found by Dr. Klauber that the specimens could readily be cleaned of tar by gasoline, so that many could be saved. An effective method for collecting museum specimens is thus indicated.

Since only the reptiles were collected quantitatively the list of specimens of other groups gives little indication of the abundance of animals that had been intercepted as they attempted

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 315.

TABLE I. *Animals collected in fresh road tar in Mohave Desert, California, June 26, 1946*

Group and species	First section 2.3 miles	Second section 3.5 miles	Total
Scorpionida			
Hadrurus hirsutus Wood	2	1	3
Vaejovis boreus (Girard)	1	....	1
Solpugida			
Eremobates pallipes (Say)	1	1	2
Orthoptera			
Anoplodusa arizonensis Rehn	1 ♀	....	1
Insara covilleae Rehn and Hebard	3 ♀s	1	4
Ateloplus notatus Scudder	1 ♂, 3 ♀s	1 ♂, 2 ♀s	7
Trimerotropis vinculata Scudder	....	1 ♀	1
Aconia integra Scudder	1 ♀	1 ♂	2
Melanoplus marginatus (Scudder)	1	....	1
Phasmida			
Parabacillus coloradus (Scudder)	1 ♂, 2 ♀s	1 ♀	4
Odonata			
Pantala hymenea Say	1	....	1
Coleoptera			
Centrioptera muricata LeConte	1	....	1
Cryptoglossa verrucosa LeConte	6	1	7
Eleodes armata LeConte	4	....	4
Sauria			
Coleonyx variegatus variegatus (Baird)	11	16	27
Callisaurus ventralis gabbii Cope	4	18	22
Urosaurus graciosus Hallowell	3	12	15
Uta stansburiana stejnegeri Schmidt	9	10	19
Phrynosoma platyrhinos platyrhinos Girard	2	5	7
Cnemidophorus tessellatus tessellatus (Say)	2	4	6
Serpentes			
Phyllorhynchus decurtatus perkinsi Klauber	4	....	4
Chionactis occipitalis occipitalis (Hallowell)	2	1	3
Crotalus cerastes cerastes Hallowell	1	....	1
Total Reptilia	38	66	104
Rodentia			
Perognathus longimembris panamintinus Merriam	....	1 ad., 3 imm.	4
Perognathus penicillatus angustirostris Osgood	....	1 ad.	1

to cross the road. The list is incomplete even for the reptiles, as numerous fragments, skeletons and scale impressions were seen. Only readily identifiable specimens were saved and many others were no doubt overlooked, because of their small size or because they had become thoroughly coated with tar. The 5.8 miles of road were covered in just 2 hours and much of the time was spent in preserving the specimens (part of the road was hurriedly covered by foot, part by one or both collectors sitting on a front fender of the slowly driven car). Scorpions, solpugids, orthopterans, and walking sticks, mostly of desert gray or tan color, and beetles, some pale and some black, were impressively numerous. It was estimated that on the average one animal per linear foot of road had become hopelessly ensnarled in the viscous road coating. Ants in uncountable numbers had swarmed in to feed on the dying and dead animals. Rodents were found in large numbers, but only a few were preserved for identification. Numerous small patches of fur gave mute evidence that much larger numbers had pulle themselves out of the tar or had been eaten b predators, grading in size from the innumerabl ants to coyotes. Traces of both mice and lizards surrounded by coyote tracks in the ta dramatically showed that these wise canines ha found many desert animals of appropriate siz ensnared in the fresh road tar. The ants ar too light, the coyotes too strong, to becom trapped.

Differences between the sections were note in the numbers of animals, particularly of th Reptilia, the only group that was rather thoroughly collected. Nearly all the small nocturnal snakes were found in section 1; those i section 2 had probably been eaten or had rolle about until they had become invisible in thei tarry coat. Desert geckos, of which the surprisingly large number of 27 was taken, wer about proportionately represented in the tw sections, but those in section 2 were dead an largely shrivelled by the oncoming heat (between 7:00 and 8:00 A.M.), whereas many c those taken in section 1 from 6:00 to 7:00 A.M. were still alive. The day-wandering lizards were, naturally, commoner in section 2. This was particularly true, despite the incomplete figures, of the large and strong whip-tailed lizards (*Cnemidophorus*), most of which, though previously stuck, struggled so violently as to escape when the collector approached. Toward the end of the collecting the tar had become sufficiently glazed so that even gridiron-tailed lizards (*Callisaurus*) and other small lizards ran across the surface.

Lizards that escape from temporary entanglement in road tar apparently survive the ordeal. Those that eluded us ran at normal speed as soon as they disengaged their bellies and legs. On June 9, 1938, on the road north from Paulden, Arizona, Laurence M. Klauber (personal communication) noticed that several of the many collared lizards (*Crotaphytus collaris baileyi* Stejneger) seen were heavily plastered below and on their feet with dried tar. They must have carried this encrustment for a considerable time, as there was no fresh tar on the road.

Obviously, nearly all of the animals listed above had become ensnarled during their normal wanderings, as had the numerous arthropods and rodents that were seen in the oil but not collected. The carnivores that were attracted to easy prey—ants and coyotes—escaped entrapment, as already indicated. Dragonflies (in part at least *Pantala hymenea*) gave the appearance of having been attracted by the similarity of the tar to a sheet of water. They hovered over the tar and seemed to be attempting to oviposit. Similar behavior by dragonflies was noted by Miller ('30) at the tar pits of Rancho La Brea.

That desert animals become entrapped in fresh road tar seems to have escaped the attention of most systematists and ecologists. Our experience, for example, was a surprise to the veteran reptile collector, Laurence M. Klauber. One reason for the failure to observe animals in the tar is the rapidity with which the trapped animals under desert conditions become completely covered by tar, shrivelled into inconspicuousness, or eaten by ants. For maximum efficiency the collecting should be done between daybreak and 7:30 A.M., while many of the animals are still alive.

Dr. Raymond B. Cowles tells us that he and his students have seen some examples of desert animals caught in road tar. He cites five rodents (*Dipodomys* and *Perognathus*) found dead and dying, by Charles H. Lowe, Jr., at 7:30 A.M. on May 30, 1946, in fresh tar at the side of the highway between Pine Valley and Laguna Junction, San Diego County, California.

Bryant ('13) reported "more than 50 pocket gophers (*Thomomys bottae bottae*) stuck in a strip of oil about two feet wide which had been left along the side of a street in process of repair in North Berkeley."

The entrapment of animals in tar pits is an old story, particularly for the Rancho La Brea tar pits near Los Angeles, where, for ages past as well as at present, mammals, birds and other animals have been lethally stuck (Merriam, '11; Swarth, '15; Stock, '30, '46). A considerable loss of birds and other animals was reported by Borell ('36) at a pit of road tar in Arizona.

The entrapment of animals in road tar is probably commoner in the desert than elsewhere. Desert heat and the nocturnal habits of most desert animals would both be conducive to such loss.

In summary, many desert animals become ensnarled in fresh road tar during their wanderings, particularly at night. Early morning collecting in such tar will provide museum material of value, readily cleaned in gasoline, and will yield data on the commonly unsuspected abundance of animal life in arid regions. Desert ecologists and collectors would profit by keeping themselves informed of the schedule of road tarring and by cruising stretches of newly tarred road, during the early morning.

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CARL L. HUBBS
BOYD W. WALKER
SCRIPPS INSTITUTION OF OCEANOGRAPHY

Contribution No. 316

NEW INTERNATIONAL ASPECTS OF OCEANOGRAPHY *

HARALD ULRIK SVERDRUP

ssor of Oceanography, Director, Scripps Institution of Oceanography, University of California

(*Read October 21, 1946, in the Symposium of the National Academy of Sciences on Present Trends and International Implications of Science*)

GRAPHY is by far the youngest member
ly of sciences which is passing review
ntil the turn of the century it was
lescriptive science, but since around
of the observed conditions in the
e been interpreted in the light of our
in physics and chemistry. Ocean-
as developed towards becoming an
ce. The development has been slow
ceanography has suffered and still
n the same conditions which admit-
existed and still exist in meteorology
were described by Angot who about
go said that too many persons take
s and too few do the thinking. The
pment can also be ascribed to the fact
en in the fields of physics and mathe-
e been attracted by the problems of

rs that now there can be anticipated
ance in applications of oceanography.
that Benjamin Franklin wrote his
er on the Gulf Stream for the benefit
s, that a century ago M. F. Maury
systematic applications of ocean-
navigation and that since around
ations to fishery problems have been
but as a new feature the last war
ed many other possible uses of peace-
rtance. In this country there has,
suddenly been created a demand for
eanographers, and I should believe
r demands have arisen in other coun-
l.

ountry the greatest single step which
ken during the past year is the estab-
a division of oceanography in the U.
Hydrographic Office, a division which
not only with the presentation of
hic information of interest to the
the Merchant Marine, but also with
sibility of carrying out basic research
s within the field of interest to those
organizations. It can be confidently expected that with more trained oceanographers available, organizations engaged in fishery research, in geological studies of the continental shelves, in studies pertaining to problems of navigation in coastal waters or to beach erosion, and the building of harbors and beach structures will make increasing use of experts.

This development will lead to an enormous expansion of activity in the field of oceanography. Before the last war it was not possible to encourage young students to specialize in oceanography because there existed only a few openings at research institutions. Now the picture is completely changed, now there is every reason to attract able students to the field because they can find employment in the applied fields or they can be attached to research establishments, depending upon their specific abilities and interests.

I am not familiar with the corresponding developments in other countries, but, judging from numerous inquiries as to the possibility of training in this country, I have reason to believe that oceanography will be advanced in nearly every country with sea borders and interests in the high seas.

Developments of this nature will make it imperative that the international cooperation in the field of oceanography be greatly strengthened in order that we can all benefit from each other's experience and in order that work carried out by different nations can be readily fitted into the world-wide pictures we hope to develop. Prior to the war there existed two world-wide international organizations which are now resuming their functions. I refer to the International Hydrographic Bureau at Monaco and to the International Association of Physical Oceanography which also deals with the chemistry of sea water and with bottom topography and sedimentation. These two organizations can be compared to the International Meteorological Organization and the International Association of Meteorology. The former, the I.M.O., is

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primarily a technical body composed of the directors of the Meteorological Services of the different countries and of a large number of specialists. It has to insure that uniform methods of observations are used, that international codes are prepared, that adequate networks of stations are established, and that the exchange of information needed in daily weather forecasting and for climatological purposes takes place smoothly. The I.M.O. functions through a number of permanent committees on which the best technical knowledge is represented, regardless of nationality.

Before the war the International Hydrographic Bureau fulfilled some of the similar functions in oceanography but the scope of its work was confined to matters of safe navigation; the membership at its conferences was restricted and its conferences were held at widely spaced intervals.

The International Associations of Physical Oceanography and of Meteorology are intended to be similar in composition and functions. They should both deal with the scientific aspects of their respective fields, but actually the Association of Physical Oceanography has taken over work which in meteorology lies within the sphere of the International Meteorological Organization and it has dealt with a number of technical questions. Obviously, one cannot and should not separate completely the research problems and the technical problems, but it should be possible to define the functions of the two bodies more clearly, and in particular to strengthen greatly the International Hydrographic Bureau and to expand the scope of its activity beyond its present limits. Such a step would, I believe, greatly benefit the scientific activity in oceanography.

I suggest that, in order to provide for smooth cooperation in all technical matters, the International Hydrographic Bureau should be organized more along the lines of the I.M.O. with the hydrographers of the different nations or their technical representatives forming a body comparable to that of directors of the Meteorological Services. In addition the organization should have a large membership, a number of standing committees, and should arrange frequent meetings. Membership in the Bureau and the Association should to a great extent overlap, in order to facilitate the equitable distribution of problems and work between the two bodies. In the future the International Hydrographic Bureau should be concerned
matters as uniformity of standard ocea
observations and uniformity of publica
should encourage different countries
pate in large enterprises or to fill in g
factual knowledge of ocean areas.
can be accomplished the Association
tinue its consideration of technical m
in the future such questions should be
the Bureau.

There exists another feature with
international cooperation which I bel
to be emphasized: To facilitate coope
oceanographic stations and institutio
adequately staffed with scientific, tec
clerical personnel. Only if this c
fulfilled can routine observations be
discussed, and published in a reason
only then can the scientific staff follo
the activities at other stations an
countries, and only then can there b
free exchange of unpublished inform
date, a very large fraction of all our
of the oceanography of the open ocea
collected on large expeditions but
from these have been painfully slow in
Each organization has been unders
advance provisions for the analysis
servations and collections and for
have generally been lacking.

Work at sea is expensive. It is po
to spend large sums on expeditio
providing funds for discussion and
And it is poor economy to maintai
small that its time must all be spent
problems, leaving little opportunity
acquainted with work that is being
elsewhere and little possibility for tra
stations and participation in congres
last remarks apply to research in
they are particularly pertinent when
sciences which are absolutely de
international cooperation. I wish t
governments which are now prepare
oceanographic research bear this
mind and that they do not embark
gram of observations without pro
which in reasonably short periods
the results of the field work and at t
keep informed as to all development

I have so far spoken in general te
now wish to illustrate the need for s
international cooperation by taking
from one of the developments du

example I have selected deals with sea, swell, breakers, and surf which war were conducted intensively in in and in this country. At that time y purpose was to prepare forecasts ns on the high seas and, particularly, ous operations. In this country the ponsored by the Bureau of Ships and raphic Office and was carreid out at Hole Oceanographic Institution and ersity of California. It is gratifying ults obtained so far are applicable to mber of peace-time problems, and gratifying that the war work has nulated the study of ocean surface kindred phenomena. So far, only a as been made; much remains to be this work international cooperation

asting technique as it stands now is he use of weather maps which give as to the wind systems over ocean ationships have been established e wind and the larger waves and, he sea raised under any given set of can be estimated. Forecasts of the sea can be made concurrently with cal forecasts. Knowing the waves sent and the laws according to which s travel through regions of calm, the f the swell reaching a distant coast puted and the time of arrival of the e forecast. In all this forecasting, eather maps are indispensable, and quirement of successful peace-time s of wave forecasting is therefore that nternational cooperation adequate ormation be obtained from the ocean h information is required in con- th the increasing aviation over the provisions are being made for main- ather ships at sea. I am therefore hat, thanks to extended cooperation orecasting, the wind systems over the e at all times well known.

ng the character of the swell that coast, however, is only part of the next step is to forecast the trans- which take place when the swell to shallow water and to estimate for locality the intensity of the wave is can be done if the effect of shoal- he configuration of the coast line and f the bottom are known. The effects of submerged ridges and of submarine canyons can be evaluated, and the often puzzling variation in the character of the breaking waves along a given beach can be accounted for.

During the war the studies were severely handicapped by the lack of reliable observations. Instruments were therefore designed for measuring waves at sea and swell off beaches. The records obtained demonstrate the extremely complicated character of the sea surface which every one of you who has recently crossed the ocean has observed. Not only do there exist waves of a large range of sizes when the wind blows, but even the most regular-appearing swell is composed of a number of wave trains.

As yet, only instruments for recording swell in shallow water have been successfully developed, using types which give a continuous record of the changing hydrostatic pressure as the swell passes over a pick-up unit at the bottom. Cables lead to shore where a photographic record is obtained, showing the variations in pressure, that is, the effect of the waves, as a boundary between the black and white parts of the paper. Every such record demonstrates the complexity of the swell. Obviously, records of this nature cannot be evaluated manually but mechanical means have to be developed by which the essential features can be obtained in a short time. An instrument for such rapid analysis was perfected in Great Britain during the war and has later been duplicated in this country, namely, an instrument for separating the periods of the recorded wave trains. This instrument renders a graph in which the wave periods appear along the abscissa and in which the ordinate gives a complex quantity depending upon the amplitude and occurrence of the different periods.

This instrument has already been used extensively and has greatly increased our knowledge of the phenomena. It has been shown that swell that travels with group velocity is preceded by long and low forerunners of periods up to 30^s. Recent studies by W. H. Munk indicate the possibility of tracking a distant storm by means of the recorded periods of these forerunners and of the local time change in the periods. The method is based upon equations which can be derived from the Hamilton-Jacobi wave equations, the contents of which have not yet been fully explored.

An analysis of the periods of the wave trains represents only the first step, however. In order to obtain a complete picture of the contents of a record the amplitude of the waves in the different trains should also be found, or, if this is impossible, other quantities which would give information about wave heights should be extracted. Only when such rapid methods of analysis have been developed will it be of advantage to establish a network of swell-recording stations, because only then can the significant wave features be obtained from the records in a reasonably short time.

This brings us to the international cooperation in this particular problem. The most urgent matter now is the problem of instrumentation which is being tackled in Great Britain and in this country, and possibly in others. Until this instrumentation has been perfected the organizations working with these instruments must remain in close contact with each other and ultimately they must agree upon specification as to the type of equipment which should be recommended for general use. When this equipment has been decided upon, the question will arise as to the establishment of an international network of swell-recording stations and as to methods of rapid exchange of information. Such a network will serve several purposes. It will render observations for further studies of the characteristics of waves at sea and for the testing of new hypotheses. It will provide data which will facilitate the analysis of ocean weather maps, data needed in forecasting of sea and swell conditions of importance to air routes over the ocean, and data indispensable to problems related to beach erosion and coastal structures. In order to achieve this end efficient and competent international organizations must direct the development.

I have so far talked exclusively about the international aspects in physical oceanography but it should, indeed, be remembered that in its broad sense oceanography comprises all marine sciences, including fisheries research. There exist several organizations which are international but not world-wide in scope and which are concerned primarily with questions in marine
biology, to which physical ocean
pears as an auxiliary science. Seve
have functioned very efficiently, but
the impression that they would ha
by having more contact with each

I suggest that it may be desirable
world-wide scientific and technical
organizations which shall deal pri
the food resources of the oceans—
under which many of those in exis
continue to function as regional
order to provide for cooperation and
ideas there should be a considerable
membership of these organizations
international bodies in physical o
One might suggest that work in al
ence be incorporated in one single
organization but this, I believe, w
practical because too many dive
would be represented. It seems be
two different groups of organi
physical-chemical-geological, and o
with overlapping memberships.

We are facing a great developm
ography leading to new internati
I may summarize these as follows:
support of oceanographic research
time nations. This support must
only for field work but also for an
cation, and travel. (2) Streng
expansion of the International
Bureau in order to achieve a broa
tion of the technical aspects of phys
oceanography, submarine topograp
marine geology. (3) Establishme
wide scientific and technical interna
izations dealing with the food res
oceans on the broadest possible bas

In conclusion, let me express the
interest in oceanography which
much advanced during these pa
years will continue to grow during
of peace, that oceanographic res
resumed by our former enemies, an
time applications will fully justify
ture of ample funds.

Contribution No. 317(1)

Reprinted from Copeia, 1947, No. 3, September 12

Ichthyological Notes

PRESENCE OF OOGONIA AND OOCYTES IN SPAWNED PACIFIC SALMON.[1]

t has been questioned whether or not all the germ-cells mature for the single spawning the Pacific salmon. In the *Journal of Morphology* (73, 1943: 207–229) I described histological changes in the testes of the sockeye salmon (*Oncorhynchus nerka*) before, ing and after the spawning and presented comparable data for the rainbow trout *lmo gairdnerii*). In the salmon as well as in the trout all the reproductive cells do mature. After the fish have spawned, there remain resting spermatogonia which in trout can form spermatozoa for the next spawning season.

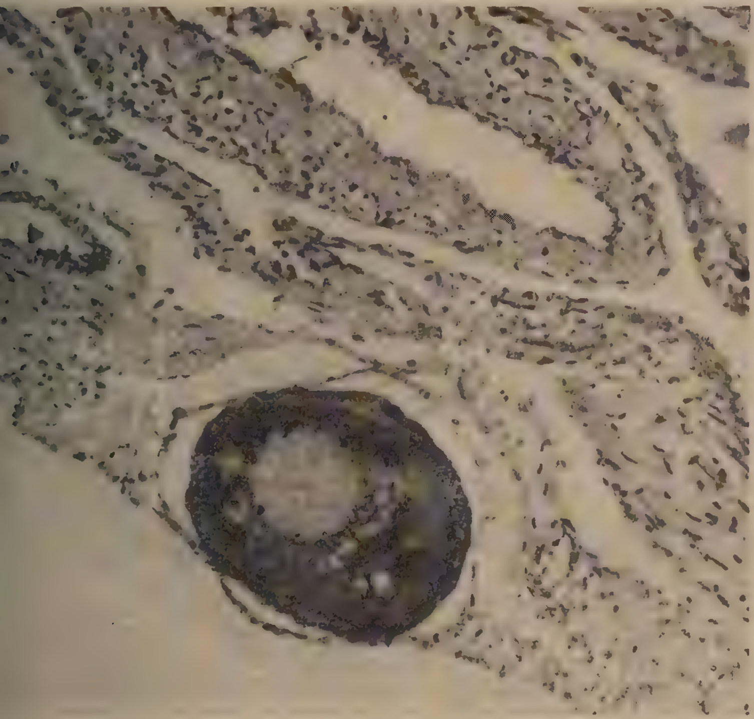

Fig. 1. Photomicrograph of a section of ovary from a post-spawning sockeye sal-n. An oöcyte 180 μ in diameter lies near the bottom of the field.

When the material for this study was gathered, a series of ovaries was also collected. is material was obtained from sockeye salmon which had been planted in Flathead ke, Montana. They formed a landlocked race in that lake. These fish arrive on the wning grounds along the gravel shores in sound condition. Soon after spawning they ibit signs of decay and they die.

Sections of ovaries from salmon which had completed spawning have from 1 to 20 ytes in each cross section (Fig. 1). The oöcytes are not atretic. They range in size from 90μ to 195μ. It is even more significant that there are in the stroma numerou cells that are characterized by a large spherical nucleus, with thread-like chromatin radia ing from the large nucleoli. These appear to be typical definitive germ-cells, in ever way similar to oögonia in sections of immature salmon and trout ovaries. Ovaries fro salmon which had spawned a few days previously are pycnotic—an indication of th general decay which sets in before death.

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[1] Contributions from Scripps Institution of Oceanography, New Series No. 317. Acknowledgment ue Dr. C. L. Hubbs for criticism of the paper.

The factor that limits the spawning of this Pacific salmon to a single season is n the potential supply of germ-cells. Were it to survive after spawning, enough germ-cel remain to replete the ovaries for another season.—George F. Weisel, *Scripps Instituti of Oceanography, University of California, La Jolla, California.*

Contribution No. 317(2)

Reprinted from Copeia, 1947, No. 3, September 12

Tirodon, a Neglected Nominal Genus of American Cyprinid Fishes[1]

By Carl L. Hubbs

N 1882 (p. 68) Oliver Perry Hay described *Tirodon*, new genus, and *T. amnigenus*, new species, on the basis of a single young minnow from Pearl iver at Jackson, Mississippi. He differentiated the genus and species from *ybognathus argyritis* (= *H. nuchalis nuchalis*) on the basis of the biserial aryngeal teeth. In 1887 (p. 251) he wrote: "It is not at all unlikely that e genus *Tirodon* (Hay, Bull. U. S. Fish Com. 1882, 68) was founded on a ecimen of this same species with an abnormal number of teeth."

Since 1887 *Tirodon amnigenus* has dropped almost entirely out of the ght of ichthyologists. It was not mentioned, even as a synonym, by Jordan d Evermann (1896–1900), nor by Jordan, Evermann and Clark (1930), r in any of the recent manuals. Fowler (1945: 25) listed it from the Pearl iver basin, as *Tirodon amnigenus*, without comment.

The problem of the identification of *Tirodon amnigenus* is of considerle significance. In the first place it is desirable to place each proposed name ther as a valid designation or as a synonym. Two statements in the original scription—"mouth rather more oblique than in *Hybognathus argyritis*" d "eye contained in the head 3 times, equal to the snout"—would, if valid, dicate that *Tirodon amnigenus* may be identical with *H. hayi* Jordan 885), over which it has priority. It is also possible, though inherently imobable, that *Tirodon amnigenus* is a valid genus and species, known only om the original account. In the second place it might be suspected from e original description and even from the specific name "*amnigenus*" that *irodon* was based on one of the numerous hybrids between genera of Amerin cyprinids. Finally, if *Tirodon* was based on a species of *Hybognathus* unexpected variation in dentition would be suggested.

In an effort to settle these questions the unique type of *Tirodon amnigenus* No. 32157) was examined at the United States National Museum in May, 933. It is a young fish, only 26 mm. in standard length, and in rather poor ndition. It was found to agree with the young of *Hybognathus nuchalis chalis* Agassiz (the subspecies of *H. nuchalis* were treated by Hubbs and agler, 1941: 50). As viewed from the side the weakly upcurved mandible very thin, but is provided with a definite symphyseal knob. The intestine of small caliber and is considerably convoluted, though it is broken and erefore is not of determinable length. In every detail of proportions, physignomy, fin position, scale size, etc., the type corresponds with the young of *. n. nuchalis*. The reputedly greater obliquity of the mouth is attributable to e condition of the specimen, for, as is often true, the muzzle was obviously unched in during preservation. Nor is the eye as large as was indicated by ay. Instead of entering the head about 3.0 times, as it does in the obliqueouthed young of *H. hayi*, the eye measures about 4.0 times in the head (to e end of the opercular membrane), as it does in the young of *H. n. nuchalis*.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 317.

Unfortunately it was not possible to verify the stated pharyngeal toot formula (2, 4—4, 2), for both lower pharyngeals had been removed. Sinc in all other respects the identity with *H. n. nuchalis* seems assured, it is concluded that the dentition was either misinterpreted (it is difficult to remov intact the arches and teeth of a 26-mm. minnow), or was highly aberran The former alternative is favored, for it is not to be expected that the oute row of teeth is ever developed in *Hybognathus*. In American minnows wit such dentition the teeth of the main row are so broad as to leave no room fo a second row to develop. In this genus and in other herbivorous genera wit like teeth, hundreds of dentitions have been examined without discoverin one that is biserial.

It is concluded that:

(1) *Tirodon amnigenus* Hay is a synonym of *Hybognathus nuchal* *nuchalis* Agassiz.

(2) The name *Hybognathus hayi* Jordan therefore retains validity.

(3) There is no good reason to suspect that *Tirodon amnigenus* w based on an interspecific hybrid.

(4) It is equally improbable that *Tirodon amnigenus* is a distinct gen and species known only from the unique type.

(5) It is more plausible that the dentition of the type was misinterpret than that it really was biserial. This idea apparently cannot be tested, sin the pharyngeal arches and teeth have become lost.

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BLIND CATFISHES FROM ARTESIAN WATERS OF TEXAS*

BY CARL L. HUBBS AND REEVE M. BAILEY

DURING the course of a collecting trip to the western and southwestern United States in 1938, the senior author visited the Witte Memorial Museum at San Antonio, Texas. Mrs. Ellen S. Quillin, the director of that institution, made available for his examination two blind catfishes (Ameiuridae) which had been pumped from deep artesian wells in the vicinity of San Antonio. Subsequently, these specimens were loaned to the Museum of Zoology. We are greatly indebted to Mrs. Quillin for placing these specimens in our hands for study. Both are now in the Witte Memorial Museum.

One of the specimens is the second known example of the remarkably specialized *Trogloglanis pattersoni* Eigenmann. The other proves to represent a distinct new genus and species apparently allied to *Pilodictis olivaris*. Other blind catfishes have been taken, but are not available. One from the artesian well of the Alamo Dressed Beef Company was presented to Witte Memorial Museum (Accession No. 25.193.37.G) but could not be found. Still others appear not to have been preserved. Thus, a blind fish from an artesian well was reported by Mrs. R. P. Persyn in the *San Antonio Light,* September 7, 1929. Mr. Josef Boecke, who collected one of the specimens described below, told us on June 3, 1938, that he had seen about twenty blind, pink catfish in the irrigation ditches fed by his artesian well, which is 1000 feet deep. Very sluggish, they were easily caught by hand. The last one seen by him was caught in June, 1934. He knew of another that came from an artesian well 1250 feet deep, west of San Antonio. It is much to be hoped that additional specimens will be preserved.

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* Contributions from the Scripps Institution of Oceanography, New Series, No. 318, and from the Museum of Zoology, University of Michigan.

The two blindcats now known from the subterranean waters about San Antonio are completely devoid of external eyes and skin pigment. That both belong to the catfish group confirms the view (Norman, 1926: 325–29; Hubbs, 1938: 266) that catfishes are particularly well represented in the subterranean fauna. *Satan eurystomus* adds not only a new genus and species to the list of blind, depigmented cave fishes, but also another line of evolution of such types. It seems to have been derived from an ancestor of *Pilodictis olivaris,* whereas *Trogloglanis pattersoni* appears to have been evolved from the *Ameiurus* type. *Satan* and *Trogloglanis* are clearly members of the North American fresh-water catfish family Ameiuridae.

The habitat of the blindcats of the San Antonio region is amazing. The specimens have come from artesian wells 1000 to 1250 feet deep. It is virtually certain that they have been derived from the chief water-bearing stratum of the region. This is the Edwards Limestone Formation of Comanche (Lower Cretaceous) age (Livingston, Sayre, and White, 1936). In the vicinity of San Antonio the top of this formation lies 400 to 1000 feet underground. Like the other formations of the region the Edwards Limestone dips toward the coast. In the southernmost part of Bexar County it lies about 3000 feet below the land surface. Farther northwest, on the Edwards Plateau, it lies at the surface. There are obviously open channels through the limestone for the artesian head closely follows precipitation. The population of the great subterranean cable. Livingston, Sayre, and White (1936: 73) wrote: depths by the ancestors of these catfishes is, therefore, expli-

> Extensive exploration by wells in this reservoir in Bexar County has shown that under large areas the limestone is traversed by an intricate system of openings. In some places the openings are small, apparently being confined to joint planes and fissures. In others they consist of solution channels of varying sizes, the largest good-sized caverns.

Since, prior to the drilling of the wells, the water in the Edwards Limestone reached the surface in large springs along Balcones Fault, and since the water in the wells now reaches to or nearly to the surface, it is obvious that the blindcats live under great hydrostatic pressure. In correlation with this habitat condition the air bladder in both species appears to have become obsolete.

Artesian waters in three prefectures of Japan have yielded a fish that is unrelated to the blindcats of Texas but parallels them in its modifications for subterranean existence. It is a member of the essentially marine family Gobiidae. Along with a similar cave form, it appears to be closely related to a common Japanese littoral goby, *Luciogobius guttatus*. The 2 subterranean, presumably fresh-water forms were very briefly described by Tomiyama (1936: 51–52, Figs. 10C–D) as variations of what he called *Luciogobius guttatus guttatus*. Regan (1941) more plausibly treated them, on the basis of Tomiyama's account, as distinct species, which he named *Luciogobius pallidus* (from the artesian wells) and *L. albus* (from a cave). They might be regarded as comprising a special genus, for they differ from the littoral gobies of the genus *Luciogobius* not only in characters associated with their dark habitats but also in an apparently trenchant feature, the lack of free pectoral rays. The cave form was described as an albino with more or less degenerate eyes. The artesian form was said to be paler and to have the eyes covered by skin. The 2 differ sharply from one another as well as from the 2 known littoral species of *Luciogobius* in body, head, and fin proportions.

This artesian-water goby and the 2 blindcats of Texas are apparently the only blind fishes that are known to inhabit artesian waters. Various other species have been reported from the outflows from artesian wells, particularly in arid regions. Some of the published accounts (listed on pages 406 and 423 in Volume III of Dean's *Bibliography of Fishes*), as well as a number of verbal reports from residents in the Great Basin, claim that the fish issued from the ground. The species concerned, with the exception of the 3 kinds under discussion, are, however, eyed and pigmented. It seems probable that their isolated distribution is attributable to some channel of dispersal other than an underground connection. Occasional surface flows of flood water readily explain some of the cases investigated afield.

Satan, new genus

Orthotype, *Satan eurystomus*, new species.

This genus is sharply differentiated from other genera of ameiurid catfishes except *Trogloglanis* by the complete absence of eyes, the obsolescence of the air bladder, and the lack of pigmentation. Despite their similarity in degenerative and adaptive features associated with subterranean life, *Satan* and *Trogloglanis* are strikingly different in many characters (Table I). Although the relationship of neither genus is fully certain, it is apparent that they represent separate evolutionary lines and that their similarities are due to convergence rather than to a common origin from a cave-adapted ancestor. *Satan* is much less modified from the surface-living ameiurids than is *Trogloglanis*. From *Ameiurus*, the presumed ancestor of *Trogloglanis*, *Satan* differs in the absence of eyes, of pigmentation, and of air bladder, in the increased size and development of the lateral line canals and pores on the head, in the reduced size of the narial apertures, in the excessive development of the adipose fin, in the reduced length of the intestine, in the more flattened and trapezoidal shape of the head, and in the broad overlapping of the branchiostegal membranes.

In superficial characters *Satan* is most closely approached by *Pilodictis*. These genera have a very similar body form, with a greatly depressed head, wide transverse mouth, slender body, and a long and flaring adipose fin. The branchiostegal mem-

TABLE I

Comparison of the Two Blind Catfishes from Texas

Character	*Satan eurystomus*	*Trogloglanis pattersoni*
Teeth on jaws	Well developed, in villiform bands	None
Jaws	Strong	Papery thin
Lower jaw	Arched, horizontal, covering premaxillary teeth	Straight and transverse, curved upward into mouth, entirely behind broad premaxillaries
Mouth	Transverse	Greatly inverted
Mouth, as seen from below	A gently arched slit	Open, semielliptical
Mouth opening inside	Scarcely restricted, more than half width of head	Greatly restricted, less than one-third width of head
End of gape	Horizontal, entirely below base of maxillary barbel	Sharply curved upward behind base of maxillary barbel
Lip at corner of gape	Thick, exposed	Thin, concealed
Nasal and maxillary barbels	Maxillary barbel very much the thicker and longer	Subequal in thickness and length
Mental barbels	Outer much thicker and longer than inner	Outer little thicker or longer than inner
Anterior nostril	A narrow tube	Broader, with a posterior flap
Posterior nostril	Small, about one-tenth internarial space; with lateral walls at base of barbel	Large, about one-fourth internarial space; lateral rim scarcely elevated
Gular fold	V-shaped	Obsolescent
Branchiostegal membranes	Broadly overlapping	Not overlapping
Angle of shoulder girdle, from below	About 50°	About 110°
Edge of shoulder girdle in front of scapular process	Scarcely arched	Strongly arched
Outer edge of testis	Finely ciliate	Weakly and sparsely lobulate
Epidermis	Velvety, easily rubbed off in preservation; hairlike cilia scarcely developed	Heavily beset with fine cilia and scattered coarse ones
Extent of visible lateral line	To below first dorsal or interdorsal space	Nearly to end of adipose dorsal

TABLE I (*Cont.*)

Character	*Satan eurystomus*	*Trogloglanis pattersoni*
Lateral line	In segments with pores at either end	Forming a keel (subcontinuous anteriorly), without well-defined pores
Lateral line pores on head	Medium to large, averaging about as large as posterior nostril; none tubular	Minute, very much smaller than either nostril; mostly in tubelets
Pore at front base of each nasal barbel	Lacking	Present
Anterior pair of mandibular pores	Opening into a common fossa	Widely separated
Snout	Greatly depressed and flat	Little depressed, broadly rounded in contour
Form of head contours from above	Isosceles trapezoid	Semioval
Free edge of rays at front margin of anal and pelvic	With very fine antrorse spinulations, several per segment	Smooth
Rays in dorsal, anal, pectoral, and pelvic fins	More numerous	Less numerous

branes are well separated and often overlap in *Pilodictis,* which in this respect furnishes, with *Istlarius,* the closest approach to the wide overlap seen in the blind genus. *Satan* and *Pilodictis* differ trenchantly, not only in those features that adapt *Satan* to life underground but also in the lack of the backward projections of the premaxillary tooth band in *Satan,* a well-developed feature in *Pilodictis.* This character varies, too, in the surface forms, since in addition to *Pilodictis* such projections occur in *Noturus,* a relative of *Schilbeodes* and, to a less extreme degree, in *Istlarius,* which is related to *Ictalurus.* In the Pimelodidae also some genera have and others lack the projections. In *Satan* the lower jaw is slightly included, whereas in *Pilodictis* it projects beyond the upper jaw, but *Satan* approaches *Pilodictis* in this character more closely than do other ameiurids.

Because of these similarities, it is suggested that *Satan* and *Pilodictis* may have had a distant common ancestry. *Pilodictis olivaris* is widely distributed in the rivers of Texas today. It is a secretive, negatively phototropic species that seeks retreat in undercut banks or beneath flat boulders, stumps, logs, or other objects. A species of such habits and with well-developed tactile senses would be expected to work into underground waters if available. The abundance of small creatures in the subterranean waters of the San Antonio area (Eigenmann, 1919: 397) would provide an adequate food supply, and subsequent modification of such an intruding population would, as usual, result in depigmentation, loss of vision, and increased development of some sense organs.

The backward projections of the premaxillary tooth band are probably to be regarded as primitive. In this respect *Pilodictis* may be more generalized than *Satan,* as it assuredly is in pigmentation, in the development of eyes and air bladder, and in the structure of the sensory system on the body. The wide separation and broad overlap of the branchiostegal membranes in *Satan* is more extreme than in other genera of ameiurids and is probably to be considered a generalized character. A seemingly parallel situation—the retention by a specialized cave fish of a primitive character that has become modified in recent surface-living relatives—has been noted by Eigenmann in the Amblyopsidae. Pelvic fins are retained in the cave-living *Amblyopsis,* whereas its closest relative in surface waters, *Chologaster,* has lost them. *Satan,* in all probability, was derived from some now extinct surface-living ameiurid not greatly different in fundamental characters from *Pilodictis.*

Certainly, neither *Satan eurystomus* nor *Trogloglanis pattersoni* is to be regarded as an immediate derivative or subspecies of its eyed ancestor, as *Typhlobagrus kronei* is supposed by Pavan (1946) to be related to *Pimelodella transitoria* or *P. lateristriga.*

WIDEMOUTH BLINDCAT

Satan eurystomus, new species

(Plate I, Figs. 1–3)

The holotype (Witte Memorial Museum, San Antonio, Texas, Accession No. 31.P.16.5) is an immature male, 68.7 mm. in standard length. It was collected near San Antonio and came from an artesian well 1250 feet deep. It was the gift of William Kempin.

Proportional measurements of the holotype, the only known specimen, are presented in Table II, and most features of body form and external anatomy are beautifully illustrated in the drawings (Plate I) prepared by Miss Grace Eager, accomplished staff artist of the Museum of Zoology. Many of the salient structural characters are indicated in the comparison with *Trogloglanis pattersoni* (Table I).

In common with most other blind, subterranean fishes, the lateral line canals and pores of the head are excessively developed. Two large pores open just behind the head, at the origin of the lateral line. The upper, more anterior one is almost level with the 2 pores comprising the straight part of the lateral line on the posterior part of the head. There are 12 large operculomandibular pores. The anteriormost pore on the mandible opens close to its fellow of the opposite side in a median transversely oval pit. A pore lies behind the eye position. Another is situated above and behind this pore. Of the 5 or 6 pores in the infraorbital series, the anterior 3 or 4 form a nearly horizontal line behind the anterior nostril. On each side there are 1 interorbital, 2 nasals, and 1 prenasal. No supratemporal canal or pores are visible. The lateral line extends to below dorsal or to below interdorsal space. It has 3 elongate pores in a short anterior tube, and behind this 5 to 9 short separated sections of tube, each with a pore on either end. Sense organs in the form of low cones are conspicuous, particularly on the head and anterior trunk regions.

The nostrils are minute. The diameter of the anterior one is about 0.4 mm., only two-fifths the size of that in *T. pattersoni.*

There are 10 branchiostegal rays. The gill-rakers on the

TABLE II

Proportionate Measurements of *Satan eurystomus* (Holotype) and *Trogloglanis pattersoni* from Near San Antonio, Texas, Expressed as Thousandths of the Standard Length

For paired structures measurements were taken on both sides and averaged.

Measurement	*Satan eurystomus*	*Trogloglanis pattersoni*
Standard length (mm.)	68.7	68.3
Body depth below dorsal origin	201	220
Body depth above anal origin, to top of adipose	174	223
Caudal peduncle depth (over-all)	104	127
Caudal peduncle depth (muscle mass only)	83	83
Caudal peduncle length	154	194
Predorsal length	343	319
Length to adipose origin	524	599
Dorsal base	133	110
Interdorsal distance	44	189
Adipose fin, basal length	371	307
Adipose fin, length to tip	381	328
Adipose notch to caudal base	127	115
Anal origin to caudal base	485	376
Anal base	234	196
Pelvic insertion to anal origin	163	162
Length to pelvic insertion	475	502
Anus to anal origin	45	63
Dorsal fin height	266	257
Dorsal spine length	105	175
Longest dorsal ray	245	225
Adipose fin, vertical height	60	86
Caudal fin length		
To upper angle	245	244
To end of shortest ray	....	212
To lower angle	238	242
Anal fin, depressed length	284	254
Longest anal ray	167	169
Pelvic fin length	136	149
Pectoral fin length	228	219
Pectoral spine length	105	174
Length first pectoral branched ray beyond tip of spine	123	45
Between pectoral insertions	224	255
From inside of shoulder girdle to tip of humeral process	47	39
Between pelvic insertions	108	102
Between pelvic fins	28	33
Head length	309	271
Head width	225	266
Head depth at occiput	182	174

TABLE II (*Cont.*)

Measurement	*Satan eurystomus*	*Trogloglanis pattersoni*
Head depth at end of first third of projection of head length	94	132
Mouth width		
Gape, exterior	159	131
Least interior width	120	81
At base of maxillary barbels, behind upper lip	154	139
Snout tip to mandible tip	8	49
Snout tip to front of gill opening	104	129
Front of gill opening to line joining pectoral insertions	146	78
Length of barbels		
Nasal	86	210
Maxillary	329	202
Outer mental	142	145
Inner mental	88	137
Distance between posterior nostrils	81	61
Snout to posterior nostril	78	58
Mandibular tooth patch, length	9	........*
Premaxillary tooth patch		
Length	11	........*
Width	126	........*

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* No teeth on jaws.

outer arch number 4 + 15 = 19. They are slender and moderately long. The longest is about one-third as long as the distance between the posterior nostrils.

The premaxillaries bear a well-developed patch of villiform teeth which form a transverse band without backward projecting processes. The length of the band is 9 per cent of the width; there is no separation or constriction at the midline. The palate is toothless.

The first dorsal fin is high and somewhat pointed, with 1 rather weak spine and 7 branched rays (counting the last 2 elements as 1 ray). The anal is long and low, with 6 unbranched and 14 branched rays. Along the front margin of the anal fin the anterior rays bear several weak antrorse spinules per segment. Except for the marginal principal rays the caudal fin is mutilated distally, but the form of the remaining part of the fin suggests that it may have been slightly emarginate. There are 17 principal caudal rays; 13 procurrent rays above, of which at least 5 are segmented; and 16 procurrent rays below, of which at least 4 are segmented. Each pectoral fin has 10 branched rays and a single spine, which is smooth along its anterior edge and bears 8 to 10 serrations posteriorly. Each pelvic fin has 9 branched rays and 1 simple ray on its outer edge, which bears spinules like those at the front of the anal fin.

The intestine is relatively thick-walled and rather short, with one extra coil about one-third as wide as the mouth. The outer edge of the testis is finely fringed, as is usual in the family. No trace of an air bladder could be found. The body cavity is largely filled with adipose tissue.

Several notable differences in form between *S. eurystomus* and *T. pattersoni* are best indicated by angle measurements (taken as described by Hubbs, 1946). In *S. eurystomus* lines joining the insertions of the pectoral fins with the point of union of the branchiostegal membranes intersect at an angle of 71°; those joining the pectoral insertion with the tip of the snout, at 51°. The angle formed by the edges of the shoulder girdle, as seen from below, is about 50°; by the edges of the gular groove, 63°; by lines joining the insertion of the pectorals and the corners of the mouth, 15°; by the dorsal and ventral contours of the head, just behind the barbels, 25°; and by the muzzle, in lateral profile, 21°.

Satan eurystomus signifies "wide-mouthed prince of darkness."

Trogloglanis Eigenmann

Orthotype.—*Trogloglanis pattersoni* Eigenmann.

This, the only previously known genus of the Ameiuridae that is wholly blind, depigmented, and subterranean, is the most sharply differentiated genus of the family. Most of its salient characteristics are given in Table I. The weak toothless mouth, much modified jaws, greatly restricted and internally situated mouth opening, foreshortened head, and obsolete air bladder, together with the modifications of the sensory system and of pigmentation, set this genus off as the most highly specialized of the Ameiuridae. Its distinctness was not fully appreciated by Eigenmann.

Eigenmann (1919: 398) suggested that *Trogloglanis* is a derivative of *Schilbeodes*. The similarity in form, in shortness of anal fin, and in certain other characters accords with this interpretation, but differentiation has proceeded so far that it is perhaps impossible to be certain of the relationships. In agreement with *Ameiurus*, as contrasted with *Schilbeodes*, the venom pore in the pectoral axil is lacking (it is present in the young only of *Ameiurus*) and the adipose fin, although large, is separated from the procurrent caudal rays. Derivation from *Ameiurus* appears to be most plausible.

Gronias nigrilabris Cope (1864: 231–32) has also been regarded as a blind cave catfish related to *Ameiurus*. The specimens, however, were caught in Conestoga Creek, Pennsylvania, and were assumed to have issued from limestone caves merely because the specimens had defective eyes. They were well pigmented and had an air bladder. We see no reason for thinking that the types of *Gronias nigrilabris* were other than specimens of *Ameiurus nebulosus nebulosus* (LeSueur) with eyes defective due to injury or some other cause. Such fish are not infrequently encountered. The serrated pectoral spine as well as the locality precludes the relationship with *Ameiurus melas* postulated by Jordan and Evermann (1896: 142). A figure of the type of *Gronias nigrilabris*, recently published by Fowler (1945: 55, Fig. 160), confirms our reference of *Gronias nigrilabris* to the synonymy of *Ameiurus nebulosus nebulosus*.

TOOTHLESS BLINDCAT

Trogloglanis pattersoni Eigenmann

(Plate I, Fig. 4)

Trogloglanis pattersoni.—Eigenmann, 1919: 397–400, Figs. 1–2 (original description; comparisons; artesian well, San Antonio, Texas). Norman, 1926: 328–29 (listed). Hubbs: 1938: 264 (listed).

The second known specimen of this species (Witte Memorial Museum, Accession No. 34.20.7.G) is an immature male, 68.3 mm. in standard length. It was caught in June, 1934, by Josef Boecke in a ditch fed by an artesian well on his ranch, 2¾ miles east and 1¼ miles north of the Alamo in San Antonio, Texas. Proportional measurements of this specimen are presented in Table II, and the peculiar mouth structure is shown in Plate I, Figure 4. Most of the more striking characters are indicated in the comparison with *Satan eurystomus* (Table I).

Though well developed, especially on the head, the lateral line system is much less conspicuous than in *Satan eurystomus*. Between a slender tube at the front of the lateral line and the uppermost pore of the opercular series, but at a distinctly higher level, are 2 similar tubules. The more posterior of the 10 or 11 small operculomandibular pores are at the tips of minute tubes. The anteriormost pore on the mandible is well separated from its fellow of the other side. There is one similar pore behind the eye position, another above and slightly behind this, 5 or 6 in the infraorbital series, 2 interorbitals, 2 nasals, 1 prenasal, and 1 more at the front base of each nasal barbel. All these pores are very minute. Most of them open in small tubules. No supratemporal canal or pores are visible. The lateral line is developed to near the posterior end of the adipose fin, but is much interrupted posteriorly. Anteriorly, it consists of an irregularly lobate dermal keel, with mere traces of open tubes and pores.

The nostrils are of moderate size. The diameter of the anterior is about 1.0 mm. It is notably larger than in *S. eurystomus*.

There are at least 8 branchiostegal rays. The gill-rakers on the outer arch number 4 + 15 = 19. They are slender, but very short. The longest is about one-seventh as long as the distance between the posterior nostrils.

The very delicate jaws as well as the bones of the palate are toothless.

The dorsal fin is high and somewhat pointed, with 1 long, well-developed spine and 5 branched rays. The anal, more or less semicircular in outline, has 4 unbranched and 11 branched rays. The outer ray is smooth. The caudal fin is weakly truncate, not convex posteriorly as shown in Eigenmann's figure (1919: 398, Fig. 1). In addition to the 17 principal caudal rays there are 13 procurrent rays above, of which 1 is segmented, and 15 procurrent rays below, of which 3 are segmented. Each pectoral fin has 9 branched rays and a single strong spine, which is smooth along its anterior edge and bears 8 or 9 prominent serrations posteriorly. The pelvic fin of the right side has 1 simple ray on its outer edge, which is smooth, and 7 branched rays.

The intestine is rather thin-walled and is somewhat more coiled than it is in *S. eurystomus.* The outer edge of the testis bears a few weak, lobulate projections, rather than the fine fringe that is usually developed in the Ameiuridae. No air bladder could be found. The body cavity is largely filled with adipose tissue.

Lines joining the insertions of the pectoral fins with the point of union of the broadly connected branchiostegal membranes intersect at an angle of 108°; those joining the pectoral insertions with the tip of the snout, at an angle of 68°. The angle formed by the edges of the shoulder girdle, as seen from below, is about 110°. The gular groove is obsolete. The angle formed by the lines joining the insertions of the pectorals and the corners of the mouth is 34°; by the dorsal and ventral contours of the head, just behind the barbels, 24°; and by the muzzle, in lateral profile, 46°.

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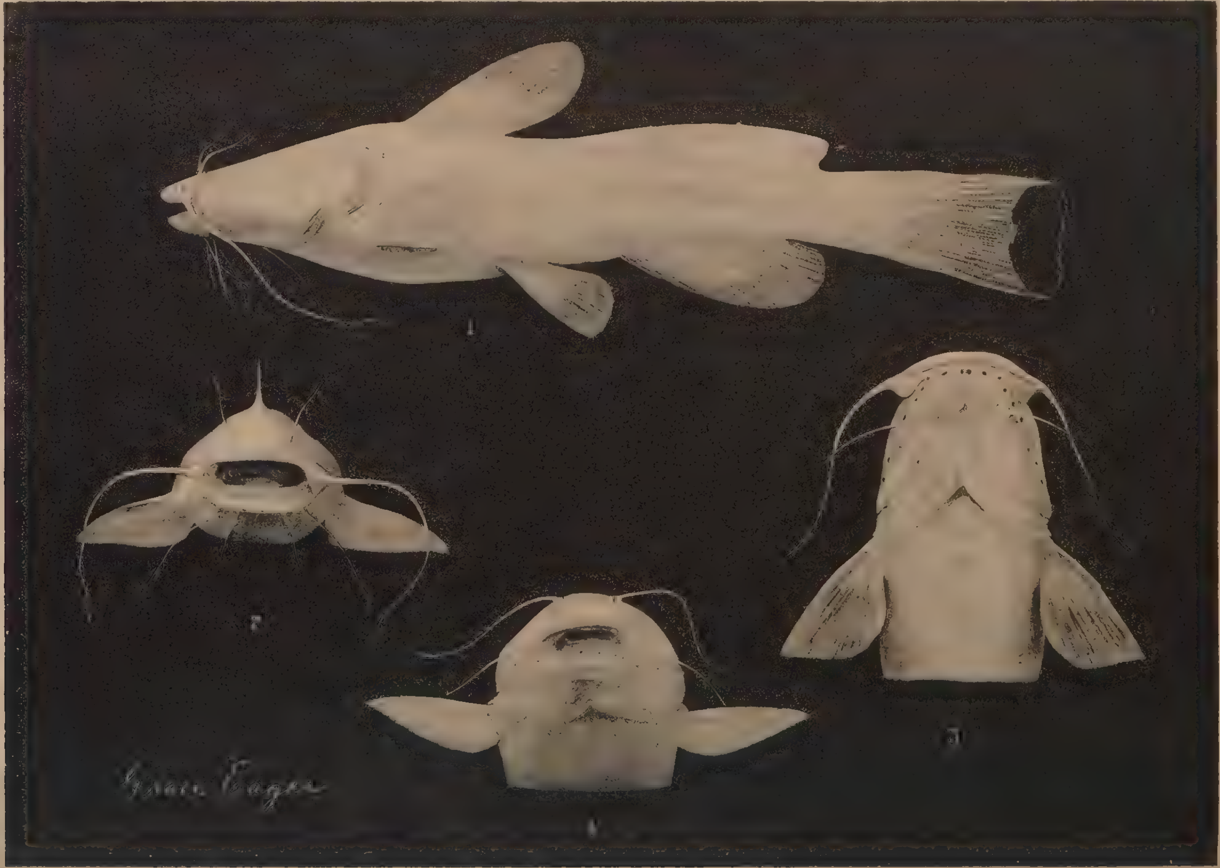
PLATE I

FIGS. 1–3. *Satan eurystomus,* holotype, in lateral, anterior and ventral aspects; standard length, 69 mm.

FIG. 4. *Trogloglanis pattersoni:* anteroventral aspect of the second known specimen; standard length, 68 mm.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15877

Attachment of Sedentary Marine Organisms to Petrolatum Surfaces.

BRADLEY T. SCHEER[*] AND DENIS L. FOX.
From the William G. Kerckhoff Marine Laboratory, California Institute of Technology, and the Scripps Institution of Oceanography, University of California.

ndependent observations, in our labora-
es, in the Clapp Laboratories, and in the
oratories of the International Nickel Com-
y, and of the Mellon Institute,[†] have
wn that sedentary marine organisms at-
much less readily to glass, metal or plas-
surfaces coated with petrolatum than to
ilar uncoated surfaces. The present pa-
presents the results of an analysis of the
onale of this effect, and certain relevant
a on the antifouling action of other com-
nds. The antifouling effect of petrolatum
ht be attributed to its unsubstantial char-
er, its hydrophobic nature, or some specific
ellant or toxic characteristic. We have
pared petrolatum mixtures of varying
sistency, and mixtures containing wetting
nts to modify the hydrophobic character;
have found no clear correlation with either
perty.

ethods. Preliminary tests with the vari-
materials were carried out in the labora-
y. Briefly, it was found that surfaces
ch permitted successful attachment of sea
mones by their bases, or of mussels by
ir byssus pads, or which permitted suc-
sful attachment or locomotion by asteroids
a stars) or gastropods (tectibranchs), were
uitable for preventing attachment of
entary organisms in general. On the oth-
hand, surfaces which prevented attachment
he test animals (*Pisaster ochraceus, Tethys*
fornicus, Cribrina xanthogrammica, My-
s californianus) in the laboratory were
n effective antifoulants.

ctual exposure tests were conducted with
s or metal plates, coated with the material
e tested, and suspended either in the open
at La Jolla or in the entrance channel to Newport Harbor at Corona del Mar. The sites and biological characteristics of the sedentary populations have been described by Coe,[1] Coe and Allen,[2] and Scheer.[3] The panels were examined at regular intervals, qualitatively at La Jolla, and semiquantitatively at Corona del Mar. Photographic records were kept of plates exposed at La Jolla.

Results. Table I gives the results of several tests with petrolatum (petrolatum white U.S.P.) In every case, coated panels were less heavily fouled than control uncoated surfaces. Two series of mixtures were then tested, to study the effects of varying consistency. These mixtures were made by diluting a crude petrolatum with lubricating oil, or with crude naphthenic acids from petroleum. The A.S.T.M. penetration values for these mixtures ranged from 93 to 450 at 77°. No consistent differences were observed in antifouling properties. However, purified white petrolatum was more effective in retarding attachment than were crude mixtures of comparable consistency.

Oil-soluble wetting agents of many different types were incorporated in petrolatum, to alter its hydrophobic properties. In an exposure at Corona del Mar, there was no relation between wettability of surface, as measured by contact angle with sea water (Adam[4]), and extent of fouling (Table II). One compound, a sodium alkyl sulfonate of uncertain composition, was markedly superior to all others tested in preventing attachment of organisms, although it was not the most effective wetting agent. Similar, though less

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Present address: School of Medicine, Univer-
of Southern California.

Personal communication from Dr. William F.
pp.

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Contributions from the Scripps
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TABLE I.

Settlement of Organisms on Aluminum Panels (A) and on Aluminum Panels Coated with Petrolatum (P) Exposed at the Same Time. Corona del Mar.†

Duration of exposure, wks	Coating	Time for 10% coverage by ABH,* days	Avg % of area covered by Bryozoans	Maximum Bryozoans	No. Tubeworms
10	A	3	18		
	P	7	0		
28	A	2	30	3	19
	P	2	0	3	2
20	A	12	5.5	41	0
	P	3	0	1	0
24	A	6	30	39	1
	P	17	0	10	2
38	A	8	28	68	9
	P	11	0	36	18
28	A	3	47	62	14
	P	5	1.1	34	29
8	A	5	1.3	110	14
	P	10	0	1	0
14	A	2	47	129	92
	P	5	0	11	2

* ABH signifies the film of algae, bacteria, and hydroids characteristic at the early stages of fouling (Scheer[3]).

† The different panels were exposed at different seasons. This accounts for the variation of intensity of settlement.

TABLE II.

Autifouling Efficacy of Surface-active Materials Incorporated in Petrolatum. Exposed at Corona Mar Beginning December 14, 1943, for 14 weeks.

					ABH		
			Contact angle		Time, wks, for coverage of		
Materials*	Chemical nature	Conc. in petrolatum %	Out	In	10%	50%	Avg covera
Aerosol-OT	Dioctyl disodium sulfosuccinate	10	45°	45°	0.65	3.2	39
Armour's AM 1180	Octadecyl amine	2	45	55	0.50	2.5	45
” ” 2180C	Octadecyl diamine and triamine	9	45	60	1.1	10.0	34
Emery's A 105 (R)	Aliphatic amine	10	45	60	0.52	2.6	48
” X 68 (R)	Aliphatic ester of polyglycol	20	45	50	2.0	8.8	29
Saponin	Phenanthrene glycoside	22	45	75	2.9	11.0	23
”	” ”	9	45	90	4.0	10.0	21
Aerosol-OT		4	60	65	1.1	11.0	29
Emery's X 72 (R)	Aliphatic ester of polyglycol	20	60	70	1.1	11.0	24
” T 333 (R)	Sodium alkyl sulfonate	20	70	70	11.0	11.0	4
Armour's AM 1120	Dodecyl amine	2	70	75	2.2	7.2	32
Emery's X 68 (R)		4	75	75	0.60	3.0	32
” ” 72 (R)		4	80	90	1.8	11.0	22
Petrolatum			90	100	1.6	11.0	22

* The trade names serve to identify the materials used; their exact composition is unknown in sev instances.

clear cut, results were obtained at La Jolla.

A second series of tests, using a series of sorbitol derivatives, confirmed the lack of correlation with wettability. The results of this series are given in Table III. The time required for development of a film of algae, bacteria, and hydroids (A B H) varied considerably among different compounds, as did the intensity of coverage and the number settlers. This variation was in no way lated to the surface action of the compoun we may note, for example, the heavy set ment on the sorbitol ether, and on the mo fied hexastearate, which differed markedly their surface action.

The results obtained in these tests sug

TABLE III.
if.ling Efficacy of Sorbitol Derivatives. Exposed at Corona del Mar Beginning July 14, 1944, for 8 Weeks. (All compounds dissolved in petrolatum to make a 10% mixture.)

Substance	Contact angle		Time, wks, for ABH coverage of		Avg coverage, %		Maximum No.	
	Out	In	10%	50%	ABH	Bryozoans	Bryozoans	Tubeworms
itan hexaoleate, modified	35°	50°	2.2	8+	12	0	3	1
itol ether	35	60	1.8	2.7	61	11	43	112
itan distearate	60	75	0.5	8+	33	8	18	12
itan oleate, modified	70	85	2.0	8+	27	0	23	0
itan monooleate	70	85	2.0	8+	20	0	6	0
itan trioleate	80	90	4.0	8+	15	0	11	0
itan triricinoleate	80	95	1.5	4.9	52	0	34	2
itan hexastearate, modified	85	95	0.4	2.0	40	26	80	34
itan tristearate	90	95	0.4	1.9	52	2.7	51	8
rolatum	90	100	0.7	8+	39	0	11	0

t the antifouling action of petrolatum
ht better be attributed to specific chemical
perties of unknown nature than to either
sistency or hydrophobic properties. Cer-
ly various modifications in chemical com-
ition produced more startling changes in
ifouling properties than did alterations in
sistency or wettability *per se*.

ne such chemical change appeared to be
thy of further examination. The most
ctive petrolatum mixtures, in the preven-
 of attachment, were those containing a
ium alkyl sulfonate. We accordingly
ed several other compounds of a similar
ure.[‡] The aliphatic sulfonates were all
y effective as antifoulants when incorpo-
ed in petrolatum, while the sulfated ester
rosol OT) was somewhat less effective;
ium hydroabietyl sulfonate was decidedly
rior.

 possible explanation of the effectiveness
the aliphatic sulfonates might be the fol-
ing: The sulfonic acid radical is polar
 strongly acidic. Accordingly, at an oil-
er interface, we would expect orientation
h that the sulfonate radical will lie in
 aqueous phase and will be ionized. This
ization will be accentuated if the solution
uffered to an alkaline pH, as is the case with sea water. This will provide, in effect, an acidic or negatively charged oil surface.

We were able to show that such orientation does occur by immersing panels coated with petrolatum-sulfonate mixtures in sea water, and measuring the change in wettability (contact angle) with time. With concentrations of sulfonate from 5 to 40%, wettability increased during the first 4 hours of immersion, rapidly at first and then more slowly. No further increase occurred during 20 hours of immersion. The importance of this orientation in prevention of fouling was shown in an experiment in which sulfonated material was mixed with a black asphalt paint. One panel was treated with this mixture and allowed to dry before immersion in sea water; a second panel was immersed in sea water for 2 hours immediately after preparation, and then allowed to dry. The second panel was distinctly superior in antifouling efficacy to the first (Table IV).

Summary. The action of petrolatum in delaying or preventing the attachment of sedentary marine organisms to submerged surfaces is not consistently altered by changes in consistency, produced by dilution with miscible liquids, or in wettability, produced by incorporation of wetting agents. The alterations observed appear rather to be the result of unknown chemical differences in the coatings. One such difference, characteristic of mixtures of petrolatum with aliphatic sulfonates, was shown to be related to orientation at the surface. It is suggested that the

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Aerosol OT (dioctyl disodium sulfosuccinate);
33 (R), T-284 (R), T-285 (R), T-286 (R)
iphatic sulfonates, Emery Industries, Inc.);
nonol X, Sulfoline P (sulfonated petroleum
ducts); Sodium hydroabietyl sulfonate (Her-
s Powder Co.).

TABLE IV.

Effect of Immersion in Sea Water on Antifouling Efficacy of a Paint-Sulfonate Mixture. Panels expos at Corona del Mar for six weeks beginning October 17, 1944.

Material	Time for 10% ABH coverage, days	Avg coverage		Maximum No.		
		ABH	Bryozoans	Bryozoans	Tubeworms	Barnac
Black asphalt paint	6	24	0	44	6	16
Same + 30% T-333	5	37	0	0	0	0
Same + 30% T-333, soaked 2 hr in sea water	14	23	0	1	0	0
Same + 50% T-333, soaked 2 hr	42+	5	0	0	0	0

interface between such a mixture and sea water has a negative charge, and that this may be important in its antifouling properties.

The authors are indebted to Messrs. Harold Schiller and Don Bowers of the General Petroleum Company of California for helpful suggestions and for assistance in the preparation of certain materials. Materials were also supplied by the Nor American Aviation Co., Emery Industries, Inc., t Atlas Powder Co., the Hercules Powder Co., t Monsanto Chemical Co., and Armour and Co. T technical assistance of Miss Margaret L. Campb was of the greatest value in a major part of t work at Corona del Mar. Helpful suggestions we made by Dr. A. C. Redfield, of the Woods H Oceanographic Institution.

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The Tsunami of April 1, 1946, in the Hawaiian Islands

G. A. Macdonald, F. P. Shepard, and D. C. Cox[1]

INTRODUCTION

unami which struck the shores of waiian Islands on the morning of 1946, was the most destructive, and he most violent, in the history of the More than 150 persons were killed, lly by drowning, and at least 161 were injured. Property damage about $25,000,000.

wave attack on Hawaiian shores was 1 uniform. The height and violence aves at adjacent points varied greatly, always in the manner which would en expected from superficial inspec- a study of the existing literature on s. Therefore, a detailed study of the f the tsunami has been made, in an understand the observed variations, the hope that the principles estab- nay help lessen the loss of life and in future tsunamis. Space is not e in the present short paper to discuss in detail, or even to present all the e for all the conclusions. These mat- be treated in detail in a longer paper d, Cox, and Macdonald, in prepara-

owledgments: We wish to thank the ersons who furnished information he course of the field study. We are ecially grateful to M. H. Carson, H. H. W. Beardin, and W. K. Sproat, pplied measurements of the high-water level in areas not visited by us; H. W. Iversen and J. D. Isaacs, who supplied additional measurements on Oahu; A. F. Robinson and Dexter Fraser, who furnished descriptions of the wave effects on Niihau and Lanai, respectively; the Hawaii County Engineer's Office, which supplied a map showing the extent of flooding in Hilo; and the U. S. Coast and Geodetic Survey, which supplied data on the earthquake and the record of the Honolulu tide gage, and permitted the use, in advance of publication, of C. K. Green's manuscript on the tsunami along the shores of North and South America. Howard A. Powers, Seismologist of the Volcano Observatory at Hawaii National Park, aided greatly in the investigation on the island of Hawaii. Miss Maude Jones, Archivist of the Territory of Hawaii, and Miss Margaret Titcomb, Librarian of the Bishop Museum, aided in locating records of past waves. C. K. Wentworth and H. S. Palmer aided greatly in discussions. Wentworth and Walter Munk read and criticized the manuscript. J. Y. Nitta prepared the illustrations.

DEFINITION OF "TSUNAMI"

The name "tsunami"[2] is applied to a long-period gravity wave in the ocean caused by a sudden large displacement of the sea bottom or shores. A tsunami is accompanied by a severe earthquake, but the earthquake does not cause the tsunami. Rather, both are caused by the same sudden crustal displacement. The waves of a tsunami have a period

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Geological Survey, Scripps Institution of aphy, and Hawaiian Sugar Planters' As- Experiment Station, respectively. This published by permission of the Director, al Survey, U. S. Department of the In-

[2] Also spelled "tunami," the Japanese equivalent of the letter *t* being pronounced *ts* in English. It appears preferable, however, to use the phonetic spelling in English, avoiding thereby much incorrect pronunciation.

of several minutes to an hour as contrasted with several seconds for ordinary storm waves caused by wind, a wave length of scores of miles as contrasted with less than 500 feet for wind waves, and a speed of hundreds of miles an hour as contrasted with less than 60 miles an hour for wind waves. Tsunamis are also sometimes termed "seismic sea waves," and are popularly known as "tidal waves." The latter term is patently undesirable, as the waves have no connection whatever with the tides. "Tsunami" is used herein in preference to "seismic sea wave" because of its greater brevity, and because the etymological correctness of the term "seismic sea wave" appears open to question.[8]

HISTORY OF TSUNAMIS IN HAWAII

Tsunamis probably reach Hawaiian shores on an average of more than one a year. Most of these are small, however, and generally escape notice except when their record is recognized on tide gages. Earlier tsunamis in Hawaii have been discussed by Jaggar (1931: 1–3) and Powers (1946: 3). The accompanying table lists all the tsunamis noticed on Hawaiian shores, in the period of written history, of which record could be found, together with their sources if known. A total of 27 are listed, or an average of one every 4.7 years since 1819. Most of them, however, did little damage. During the same interval there are listed five severe tsunamis which caused extensive damage, an average of one every 25.6 years.

Other violent waves have been termed "tidal waves" in the newspapers, but were more probably storm waves. Such were the wave which hit Maliko, Maui, on January 28, 1895, and those which struck Kaumalapau on Lanai, and Nawiliwili on Kau May 30, 1924.

It will be noted that only two of t tsunamis listed in the table were of origin. With the exception of the nun volcanic earthquakes on the island o waii, which seldom cause tsunamis Hawaiian region is only moderately seismically (Gutenberg and Richter, 84–85). The great majority of the tsu reaching Hawaii originate in the seismic border zone of the Pacific. 22 tsunamis from known sources lis the table, five came from near South ica, one from near Central America from near California, three from near and the Aleutian Islands, five from Kamchatka, three from the Japanese and one from near the Solomon Island the five severe tsunamis, three orig

TABLE 1

Hawaiian Tsunamis

DATE	SOURCE	DAMAGE IN HAWAII	A SP V
	nearest coast		mi
1819 Apr. 12	Unknown	Unknown	
1837 Nov. 7	South America	Severe	
1841 May 17	Kamchatka	Small	
1868 Apr. 2	Hawaii	Severe	
1868 Aug. 13	South America	Severe	
1869 July 25	South America (?)	Moderate	
1872 Aug. 23	Hawaii	Small	
1877 May 10	South America	Severe	
1883 Aug. 26	East Indies	Small	
1896 June 15	Japan	None	
1901 Aug. 9	Japan (?)	None	
1906 Jan. 31	Unknown	None	
1906 Aug. 16	South America	Small	
1918 Sept. 7	Kamchatka	Small	
1919 Apr. 30	Unknown (distant)	None	
1922 Nov. 11	South America	None	
1923 Feb. 3	Kamchatka	Moderate	
1923 Apr. 13	Kamchatka	None	
1927 Nov. 4	California	None	
1927 Dec. 28	Kamchatka	None	
1928 June 16	Mexico	None	
1929 Mar. 6	Aleutian Is.	None	
1931 Oct. 3	Solomon Is.	None	
1933 Mar. 2	Japan	Small	
1938 Nov. 10	Alaska	None	
1944 Dec. 7	Japan	None	
1946 Apr. 1	Aleutian Is.	Severe	

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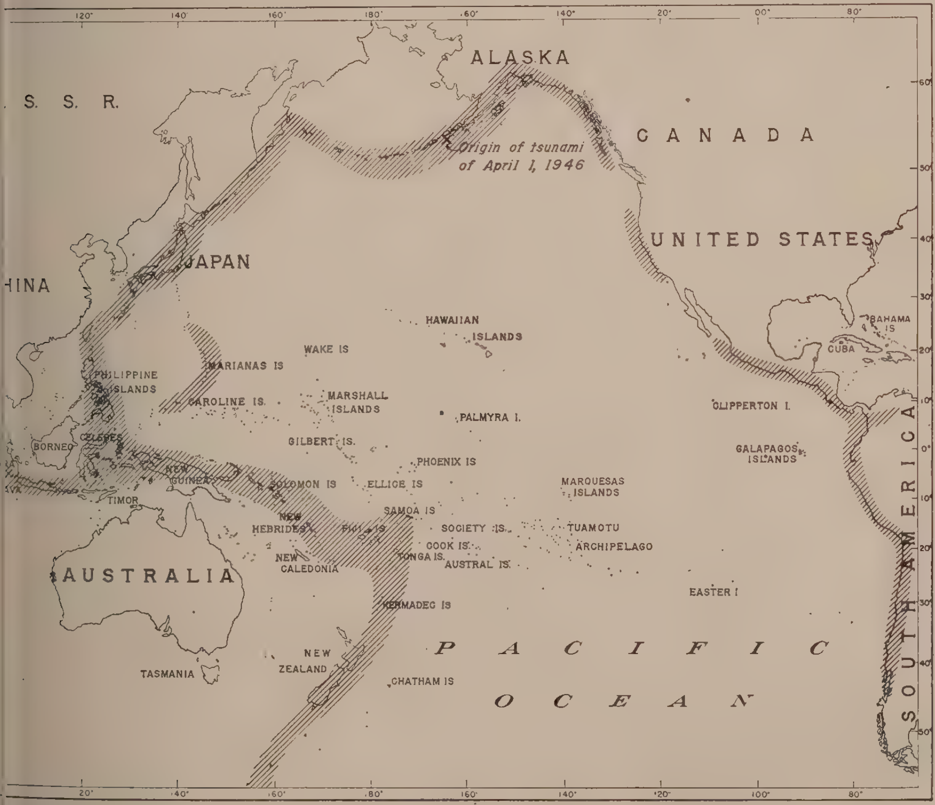
[8] The adjective "seismic" is derived from the Greek root *seismos,* meaning earthquake, and is defined as pertaining to, produced by, or characteristic of an earthquake. The waves in question are not, however, characteristic of most earthquakes, even those of submarine origin, and are not produced by earthquakes.

the coast of South America and one in Aleutian area, and one was of local ı. One tsunami of moderate intensity from near Kamchatka, and another ıbly from South America.

ERAL FEATURES OF THE APRIL, 1946, TSUNAMI: ORIGIN AND NATURE OF THE WAVES

ıe tsunami of April 1, 1946, was caused movement of the sea bottom on the ıern slope of the Aleutian Deep, south nimak Island. The same crustal move- gave rise to a violent earthquake, re- :d on seismographs all over the world. In Hawaii, it was recorded on the instrument of the U. S. Coast and Geodetic Survey located on the campus of the University of Hawaii in Honolulu, and on those of the Hawaiian Volcano Observatory at Kilauea on Hawaii. The epicenter of the earthquake has been located by the Coast and Geodetic Survey at latitude 53.5° N. and longitude 163° W., and the time established as 1^h 59^m A.M. Hawaiian time (12^h29^m Greenwich time) (Bodle, 1946: 464). It may be assumed that the tsunami originated at the same place and time as the earthquake. The place of origin was thus 2,241 miles N. 8.5° W. of Honolulu, and 2,375 miles N. 12° W. of Hilo (Fig. 1).


120°
140°
160°
180°
160°
140°
120°
100°
80°
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
ALASKA
S. S. R.
CANADA
Origin of tsunami of April 1, 1946
UNITED STATES
JAPAN
HINA
HAWAIIAN ISLANDS
BAHAMA IS
CUBA
WAKE IS
MARIANAS IS
PHILIPPINE ISLANDS
CAROLINE IS.
MARSHALL ISLANDS
PALMYRA I.
CLIPPERTON I.
BORNEO
CELEBES
GILBERT IS.
PHOENIX IS
GALAPAGOS ISLANDS
NEW GUINEA
SOLOMON IS
ELLICE IS
MARQUESAS ISLANDS
TIMOR
SAMOA IS
NEW HEBRIDES
FIJI IS
SOCIETY IS.
TUAMOTU ARCHIPELAGO
COOK IS.
NEW CALEDONIA
TONGA IS.
AUSTRAL IS.
AUSTRALIA
EASTER I
KERMADEC IS
SOUTH AMERICA
PACIFIC
NEW ZEALAND
TASMANIA
CHATHAM IS
OCEAN

ı. 1. Map of the Pacific basin, showing the position of the Hawaiian Islands, the place of origin e tsunami of April 1, 1946, and the distribution of seismically active belts around the Pacific in ı tsunamis are likely to originate.

The time of arrival of the waves in the Hawaiian Islands is known with certainty only at Honolulu. The record of the Honolulu tide gage (Fig. 2) shows that the first rise started at about 6:33 A.M. (Green, C. K., 1946: 491), though the exact time cannot be stated closer than 2 or 3 minutes. The drum of the water-stage recorder at the Waimea River, on Kauai, revolves too slowly to give an accurate indication of time, but the first rise appears to have started there at about 5:55. At Hilo, electric clocks were stopped at 7:06, and a brief power failure occurred at 7:18. These have been interpreted by Powers (1946: 2), probably correctly, as the time of arrival of two wave crests at Hilo. From other considerations, discussed briefly elsewhere (Shepard, Macdonald, and Cox, in preparation), it appears probable, however, that the crest at 7:06
was the second wave at Hilo, not the
If so, allowing for the observed 15-m
interval between later waves, the first
at Hilo probably started at about 6:45. (
puted from these times of arrival, th
proximate average speed of the tsunami
its origin to Honolulu and Hilo was, re
tively, 490 and 498 miles an hour. O
tering shallow water the waves decr
greatly in speed. The waves movin
Kawela Bay, on Oahu, were estimate
Shepard to be moving only about 15
an hour. Similar low speeds near shore
reported by other observers, and are
parable to the speed of 20 miles an
recorded in San Francisco Bay (G
C. K., 1946: 492).

The interval between the first and
wave crests, as recorded on the Honolulu
gage (Fig. 2), was about 25 minutes,

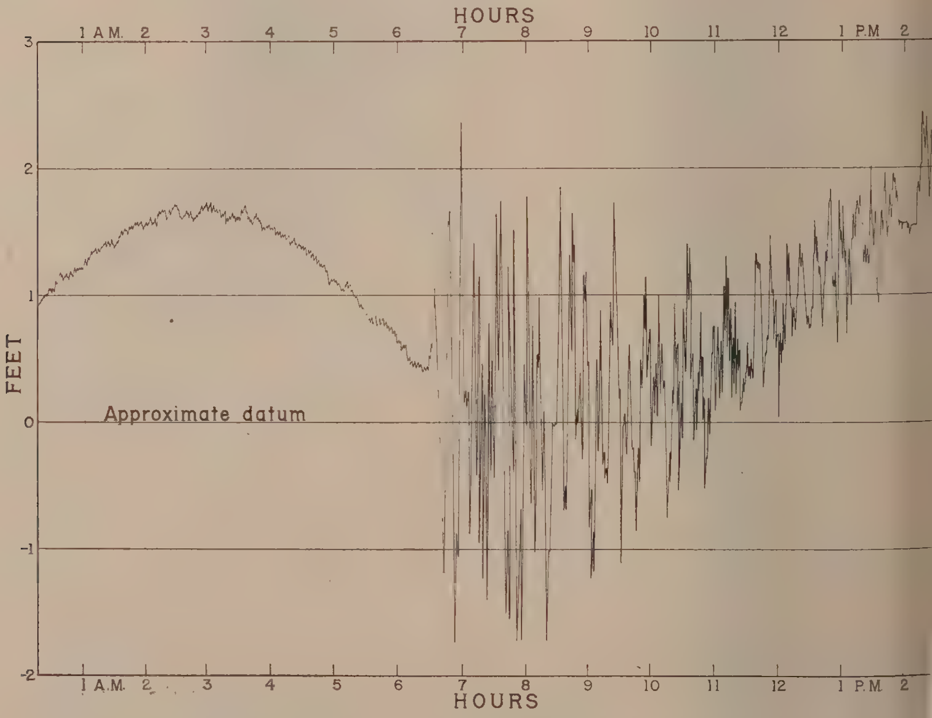


FIG. 2. Record produced on the tide gage in Honolulu Harbor by the tsunami of April 1, 1

an average interval between early wave of approximately 12.5 minutes. The l between the first wave crest and the ding trough was 7.5 minutes, however, ting a wave period of 15 minutes at ginning of the disturbance. This cor- ds with the mean wave period of 15.6 es found by Green (1946: 499) at ulu and eight other stations on the of North and South America. At the of Nuuanu Stream in Honolulu, C. K. worth observed an interval of approxi- 15 minutes between successive bores ing the stream, and a wave period of 15 minutes was observed by J. B. Cox . C. Cox at Waikiki at about 7:45 A.M. vations elsewhere were poor, but in l indicated an interval not far from nutes between the early waves of the The interval between later waves at ulu (Fig. 2) and elsewhere was r and less regular, probably because of rival of chains of waves traveling by hat different routes, refracted around nt sides of islands, and reflected at s points, as well as traveling by the direct route. Probably contributing to regularity of later waves were wind and also the free-period oscillations, bors and channels, known as "seiches." period of the waves is assumed to be inutes, and the average speed to be 489 miles an hour, the average wave from crest to crest was about 122

ect observations on the height of the in the open sea are lacking, but theo- considerations indicate that the height bly did not exceed 2 feet from crest ugh.[4] If so, the small height combined he very great wave length should have the waves imperceptible to ships at sea. such was indeed the case is indicated by the fact that the master of a ship lying offshore near Hilo could feel no unusual waves, although he could see the great waves breaking onshore. Crews of fishing boats in the Hawaiian area also reported no unusual conditions at the time of the tsunami, although heavy storm waves were running. The few reports of violent waves of great height from ships at sea were probably occasioned by storm waves, together with the knowledge that a tsunami was taking place.

The nature of the waves sweeping up on to Hawaiian shores varied greatly from place to place. At some places the water rose gently, flooding over the coastal lands without the development of any steep wave front. At such places most of the damage resulted from the violent run-back of the water to the sea. At some localities, although the general water surface rose gently, ordinary storm waves moved in over the top of the broad swells of the tsunami, and there at least part of the damage was caused by the storm waves. At most places, however, the waves of the tsunami swept toward shore with steep fronts and great turbulence, causing a loud roaring and hissing noise. Locally, the wave closely resembled a tidal bore, the steep front rolling in over comparatively quiet water in front of it. Behind the steep front, the wave crest was broad and nearly flat, with smaller storm waves superimposed upon it. Such bores were best developed in bays and estuaries, but waves of closely similar form were observed crossing shallowly submerged reefs upon otherwise open coasts.

At many places the violence of the waves moving shoreward was sufficiently great to tear loose heads of coral and algae, up to 4 feet across, and toss them onto the beach as much as 15 feet above sea level. Locally, blocks of reef rock weighing several tons were quarried at the outer edge of the reef and thrown onto the reef surface.

Between crests, the water withdrew from shore, exposing reefs, coastal mud flats, and

---

sed on the assumption of a 10-foot wave in t of water, and the variation of the wave inversely as the fourth root of the depth.

harbor bottoms for distances up to 500 feet or more from the normal strand line. The outflow of the water was rapid and turbulent, making a loud hissing, roaring, and rattling noise. At several places houses were carried out to sea, and in some areas even large rocks and blocks of concrete were carried out onto the reefs. Sand beaches were strongly eroded by the outgoing water. People and their belongings were swept to sea, some being rescued hours later by boats and life rafts dropped from planes.

At a few places, generally but not exclusively on the sides of the islands away from the wave origin, the first wave was reported to have been the highest. At those places, the rise was generally of the quiet sort. There are, however, no instrumental records showing the first wave to have been the highest, and it is possible that at places reporting the first wave as the highest, earlier waves may have been overlooked. Much more generally the third or fourth wave was reported to have been the highest and most violent. The third crest was the largest at the Honolulu tide gage (Fig. 2). At other localities the sixth, seventh, or eighth waves were said to have been the highest. At Waimea River, Kauai, the sixth crest was higher than any other, both in absolute level and in its height above the preceding and succeeding troughs.

In general, if not everywhere, the size and violence of the waves increased to a maximum with the third to eighth waves. The oscillations then gradually decreased in amplitude over a period of at least 2 days, but with occasional waves which were larger than those just before and after them. Such temporary increases in wave height probably resulted from mutual reinforcement by the essentially simultaneous arrival, in phase, of waves which had traveled different paths, or from the coincidence of tsunami waves with storm waves or seiche oscillations.

Measures of the height of the waves approaching shore in shallow water, but before they dashed up on shore, are poo
Kawela Bay, Oahu, Shepard estimat
height of the waves advancing across t
to have been as much as 18 feet, and
ers estimated the height of the waves
ing the reef off Lanikai, on Oahu, t
been about 7 feet. Photographs taken
show the top of the breakers to have b
feet above the normal bay surface whe
struck Cocoanut Island, but the wav
have increased considerably in hei
crossing the breakwater, and the ef
dashing up on the shore was probably
present, further exaggerating the
Photographs of some of the late waves
mouth of the Wailuku River, in Hilo
them to have been 6 to 8 feet high
8), and early waves undoubtedly
higher. In general, these heights corr
fairly closely with the measured hei
which the water dashed on the shore a
localities. At any rate it appears cle
the waves not only slowed down,
creased in height on entering shallow
George Green (1838: 457–462) stat
the wave height varies inversely as the
root of the depth of the water.

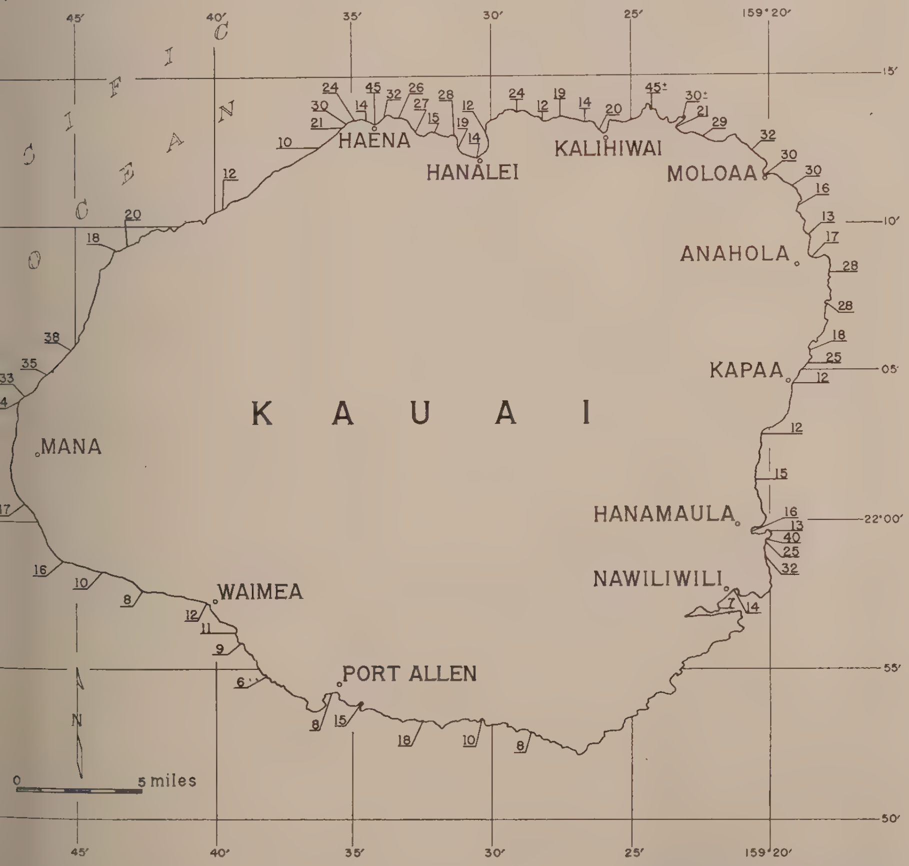
Most observers reported the first
ment on Hawaiian shores to have
withdrawal of the water. However, th
available instrumental records, at Ho
and Waimea, both indicate the first
ment to have been a rise. The instru
records are probably more reliable th
reports of untrained observers. The
rise at Honolulu was small (Fig. 2),
similar small rise at other localities m
ily have been overlooked. Certainly it
have been less impressive than the
withdrawal of the water from shore
succeeding trough approached. It is
esting to note that the records of tide
along the coasts of North and South A
obtained by C. K. Green (1946: 49
show the initial movement to have

ith amplitude of about one third that ensuing trough.

EIGHTS REACHED BY THE WAVES ON HAWAIIAN SHORES

surements of high-water marks have nade around the shores of all five islands of the Hawaiian group. The ed heights are shown on Fig. 3 to 7. ights are stated in feet above lower ater. At each point sea level was esti- the height of the high-water mark that level was measured by means of evel or steel tape, and the measurement reduced by means of tide tables to height above lower low water. Some inaccuracy undoubtedly has entered in the estimation of mean sea level, but it is believed that the heights are probably accurate to within 1 foot. The levels measured include: points indicated by eyewitnesses as the upper limit of the water, lines of flotsam or swash marks, the upper limits of soil and vegetation scouring, levels of consistent scratching and barking on trees, and the upper level of staining on the walls of buildings.

The measured heights of high-water marks range from 55 feet at Pololu Valley


45′
40′
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05′
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55′
50′
PACIFIC
OCEAN
KAUAI
HAENA
HANALEI
KALIHIWAI
MOLOAA
ANAHOLA
KAPAA
HANAMAULA
NAWILIWILI
PORT ALLEN
WAIMEA
MANA
24
30
21
45
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32
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17
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33
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38
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5 miles
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3. Map of the island of Kauai, showing heights reached by the water during the tsunami of , 1946. Heights are in feet above lower low water.

on Hawaii, 54 feet at Waikolu Valley on Molokai, and 45 feet at Haena and Kilauea Point on Kauai, to 2 feet at Kaunakakai on Molokai, 2 feet at Milolii and Hoopuloa on Hawaii, and less than 2 feet at the head of Kaneohe Bay on Oahu. Causes of the variations in height will be discussed in a later section.

Most of the heights measured are, of course, not the heights of the actual waves, but rather the heights to which the water was driven on shore. On a vertical cliff directly across the path of the wave, this height may theoretically amount to twice the height of the actual wave. On slopes less than vertical, or on cliffs at an angle to the direction of wave advance, it should be somewhat less than twice the wave height. This measure represents the height of dash of solid water, but very abundant spray may be thrown much higher. Moreover, storm waves riding on the crest of the broader swells of the tsunami undoubtedly added in places to the height to which water dashed on shore. There are places where normal trade-wind waves are flung to a height nearly as great as that reached by the tsunami, and many places, particularly on shores facing away from the origin of the tsunami, where waves of heavy storms reached appreciably higher than did the waves of the tsunami.

It is not possible to make reliable estimates of the magnitudes of these complicating factors, as there are too many unknown elements involved. However, it is probable that most of the water heights recorded for the tsunami on the northern and eastern sides of the islands were appreciably increased by these factors.

FACTORS INFLUENCING THE HEIGHTS AND INTENSITIES OF THE WAVES

It may be assumed that the size and speed of the waves approaching the islands from the open ocean to the north were essentially the same throughout the length of the Hawaiian Archipelago. Differences in h reached by the water and in violence of attack along Hawaiian shores must b tributed to local influences modifyin size and behavior of the waves.

The factors found to have affecte height and intensity of the waves durir tsunami of April 1, 1946, are:

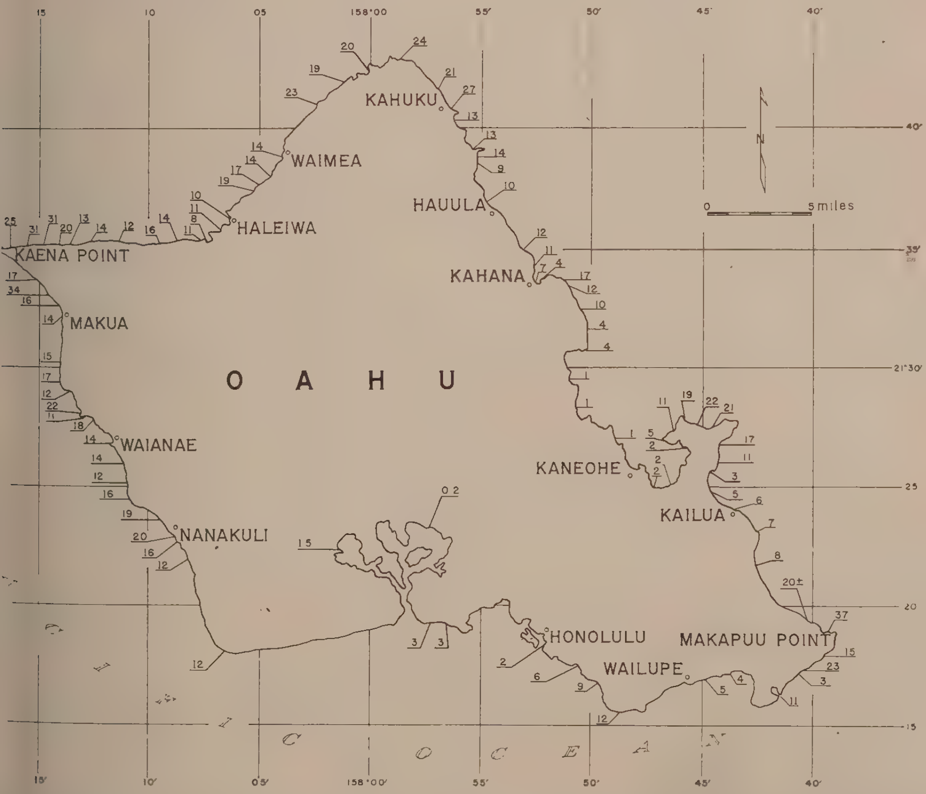
1. Orientation of the coast line with r to the point of origin of the tsunan
2. Shape of the island.
3. Exposure to storm waves.
4. Submarine topography.
5. Presence or absence of reefs.
6. Configuration of the coast line.
7. Merging of waves from different tions, or of different types.

Orientation of the coast line with resp the point of origin of the tsunami.—Ir eral, the heights reached by the water greatest on the sides of the islands the origin of the waves, and lowest c sides away from the wave origin. T evident from even a cursory inspecti the maps (Fig. 3 to 7). Heights a consistently greater on the northern th the southern sides of the islands. A extreme heights were measured on the ern or northeastern sides. Conversely of the lowest figures were found c southern and southwestern sides. It a almost self-evident that this should Waves striking northern shores retair full force, whereas the refracted waves ing southern shores suffer a diminut force and height. This effect is discuss wind waves in *Breakers and surf* (U. S Hydrographic Office, 1944: 12–13) wave can be refracted or reflected w losing some of its force.

Shape of the island.—Waves were re around circular or nearly circular much more effectively than around a or elongate islands. This fact had a r effect on the height and violence of w

uthern shores. Thus the water reached
lerably greater heights along the south-
oast of the nearly round island of
i (Fig. 3) than along the southern coast
e angular and elongate island of Molo-
Fig. 5), even though the heights along
orthern coast of Molokai were on the
ge perhaps a little greater than those
e northern coast of Kauai. The contrast
en the very high average height on the
ern coast of Molokai and the very low
ge height on the southern coast is
r than that between the two sides of
ther island, although the difference
en the extreme highs and lows is al-
exactly the same as on the island of
ii (Fig. 7).

Exposure to storm waves.—At the time of the tsunami, large storm waves had been running for several days. As already pointed out, these storm waves riding in on the backs of the broad swells of the tsunami in places undoubtedly increased the height to which the water dashed on shore. Moreover, in other places, where the rise in water level due to the tsunami was gentle, storm waves on top of the tsunami were responsible for much of the damage. The generally greater violence of the waves on the windward (northern and northeastern) coasts as compared to that on the leeward coasts may have been in considerable part the result of the large storm waves which were driving in on the windward coasts. Places on the wind-


15
10
05
158°00
55′
50′
45′
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20
24
19
21
23
27
KAHUKU
13
13
14
14
WAIMEA
14
17
9
19
10
10
HAUULA
11
8
HALEIWA
25
31
31
20
13
14
12
16
14
11
12
11
KAENA POINT
7
4
KAHANA
17
34
16
17
12
10
14
MAKUA
4
4
15
17
O A H U
12
22
11
18
14
WAIANAE
11
19
22
21
5
2
17
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12
16
KANEOHE
2
2
3
5
6
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KAILUA
7
19
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NANAKULI
15
16
12
8
20±
37
3
3
HONOLULU
MAKAPUU POINT
15
12
2
6
9
WAILUPE
23
3
4
5
11
12
O C E A N
0
5 miles
N
40′
35′
21°30′
25
20
15
15′
10′
05′
158°00′
55′
50′
45′
40′

4. Map of the island of Oahu, showing the heights reached by the water during the tsunami
ril 1, 1946. Heights are in feet above lower low water.

ward coasts which were sheltered from the storm waves also experienced less violent waves. Thus at Kalaupapa, on the sheltered side of the peninsula on the windward side of Molokai, both photographs and the testimony of observers indicate that the rise of 25 feet caused by the tsunami was not violent. On the windward coasts, much of the rapid variation in intensity of wave attack may have resulted from the caprice of storm waves.

Submarine topography. — Owing to their great wave length, the waves were somewhat affected by the ocean bottom throughout their course. However, the effect of the bottom increased greatly as the waves moved into shallow water, and caused a slowing of the wave, an increase in its height, and a steepening of its front. A direct evidence of the increase in height of the waves in shallow water was afforded by the lesser heights reached by the water at the ends of certain peninsulas projecting into deep water and not prolonged seaward by pronounced ridges, as compared with the heights on adjacent shores rising from shoal water. Thus at the end of Kalaupapa Peninsula, on the northern coast of Molokai (Fig. 5), the water dashed only 7 feet above normal sea level, distinctly less than do the waves of ordinary storms; whereas on the coas ing from shoal water both east and w the peninsula, the water swept up to h of 30 to 54 feet. At the end of Keana insula, on the northern coast of Maui 6), the tsunami reached heights only greater than large trade-wind waves.

Submarine ridges and valleys, partic those pointing toward the wave source of great importance in their effect strength of the waves. The best exam the effect of ridges are found on the ern coast of Kauai. A long ridge e in a direction slightly west of north Haena, to a depth of about 8,00 (Plate 2). Another extends northea from Kilauea Point, to even greater d The greatest heights (45 feet) reach the water on the shores of Kauai w the heads of these two ridges (Fig. 3) other ridge extending northwestward the western coast of Kauai is probab sponsible for heights of 35 to 38 feet head. Long ridges projecting from and Kahuku Points on Oahu similarly an increase in wave heights there as pared to the heights on both sides (Fi The ridges projecting eastward north o Bay and at Cape Kumukahi on Hawai on the other hand, no such pron

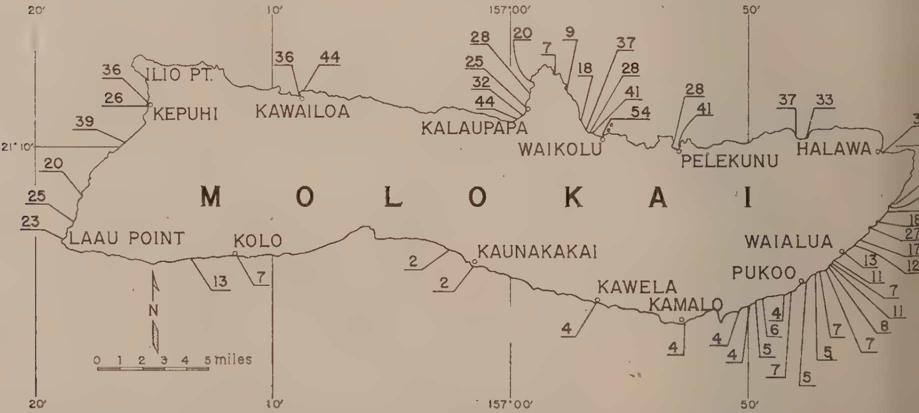


FIG. 5. Map of the island of Molokai, showing heights (in feet above lower low water) r by the water during the tsunami of April 1, 1946.

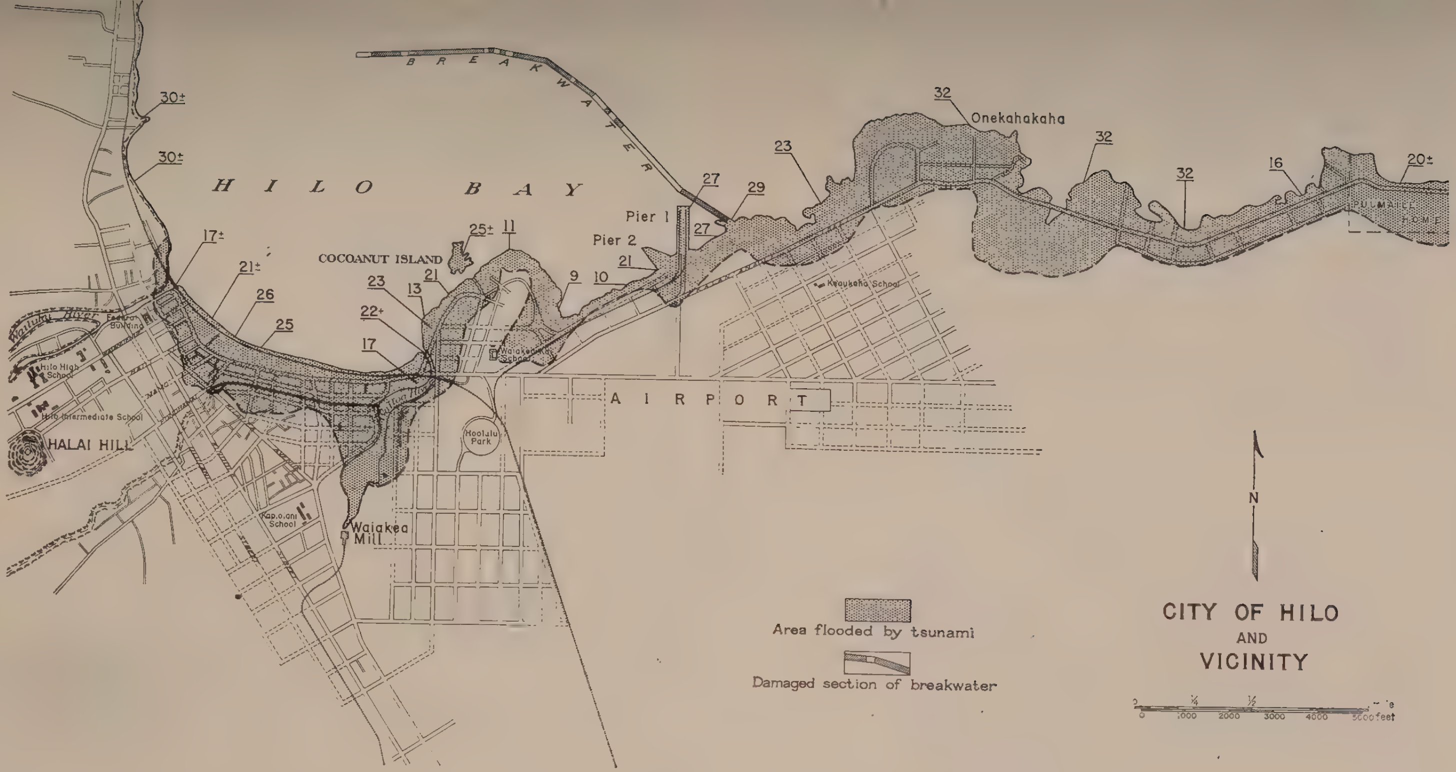
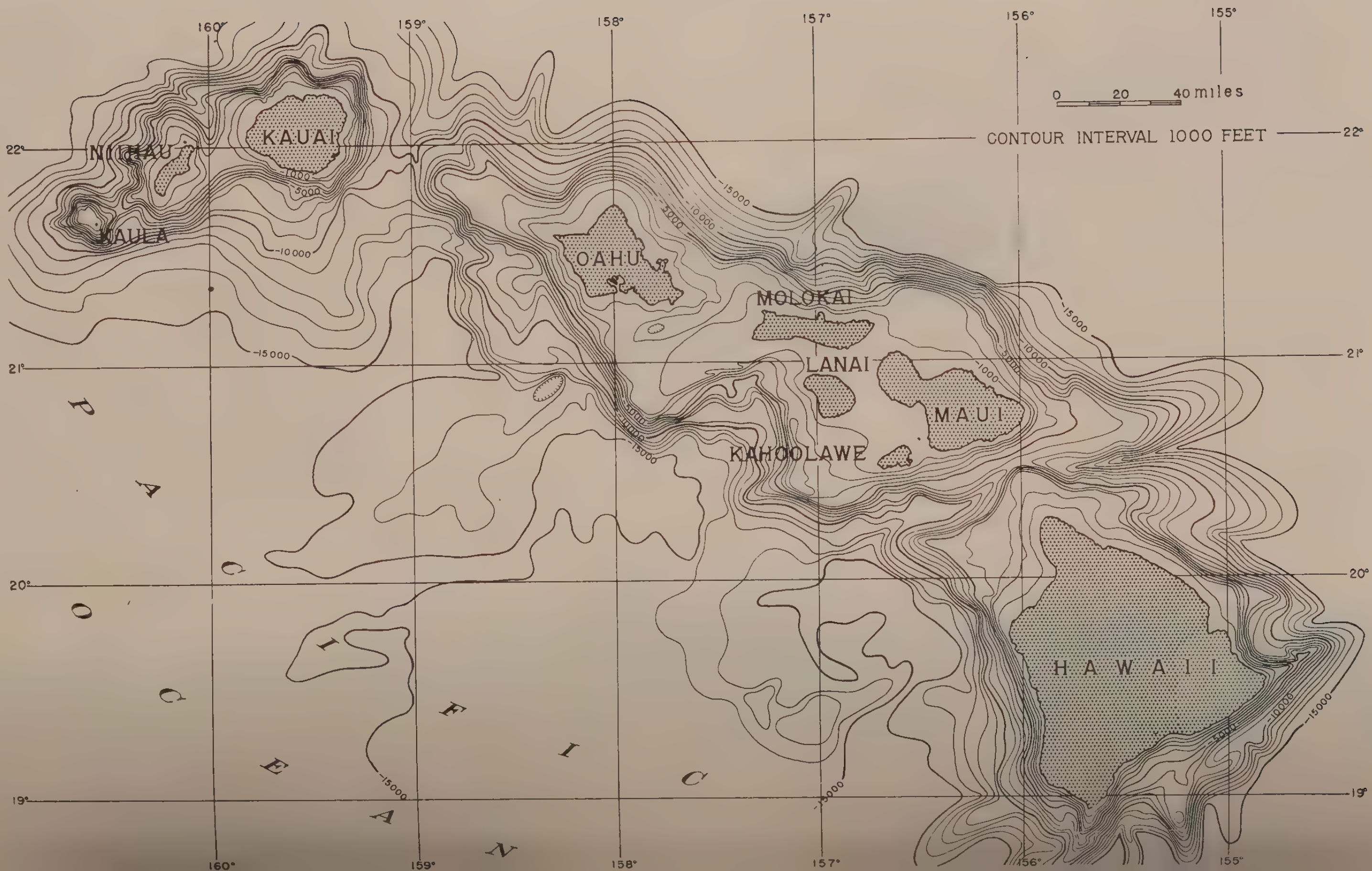
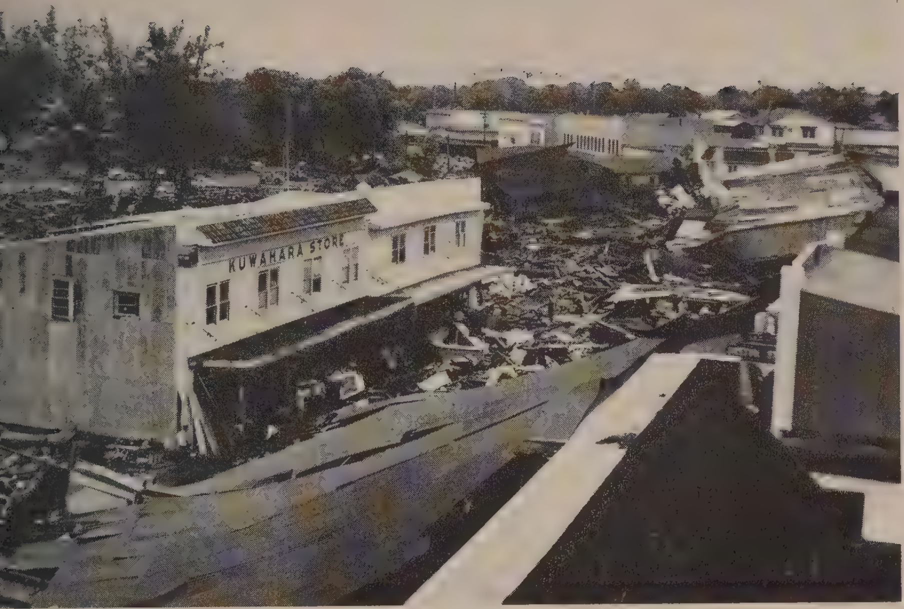
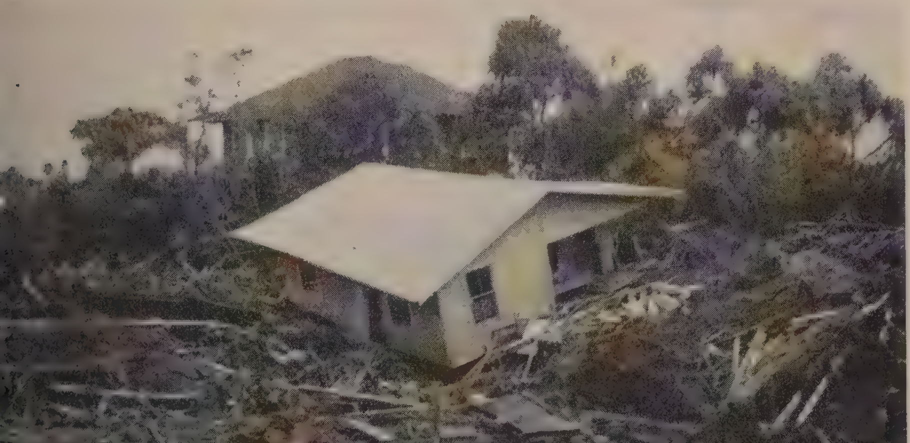

30±
30±
BREAKWATER
HILO BAY
17±
21±
26
25
COCOANUT ISLAND
25±
11
23
13
21
22±
17
9
10
Pier 1
Pier 2
21
27
27
29
23
32
Onekahakaha
32
32
16
20±
PUUMAILE HOME
Wailuku River
Federal Building
Hilo High School
Hilo Intermediate School
HALAI HILL
Kapiolani School
Waiakea Mill
Hoolulu Park
Waiakea School
Keaukaha School
AIRPORT
N
Area flooded by tsunami
Damaged section of breakwater
CITY OF HILO
AND
VICINITY
0
¼
½
Mile
0
1000
2000
3000
4000
5000 feet

PLATE 1. Map of the Hilo area on the island of Hawaii, showing the heights reached by the water, the area of flooding, and the portion of the breakwater destroyed (shaded portions) during the tsunami of April 1, 1946. Heights are in feet above lower low water.


160°
159°
158°
157°
156°
155°
0 20 40 miles
CONTOUR INTERVAL 1000 FEET
22°
21°
20°
19°
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
KAHOOLAWE
HAWAII
1000
5000
10000
15000
PACIFIC OCEAN



E 3A. Wreckage left by the tsunami along Kamehameha Avenue, Hilo. Buildings on the left- seaward) side of the street have been pushed into the street, some more or less intact, others s of debris. Photo by Francis Lyman.



E 3B. House in Keaukaha, east of Hilo, carried inland about 100 feet by the waves. The in the background was above the reach of the water. Photo by G. A. Macdonald.

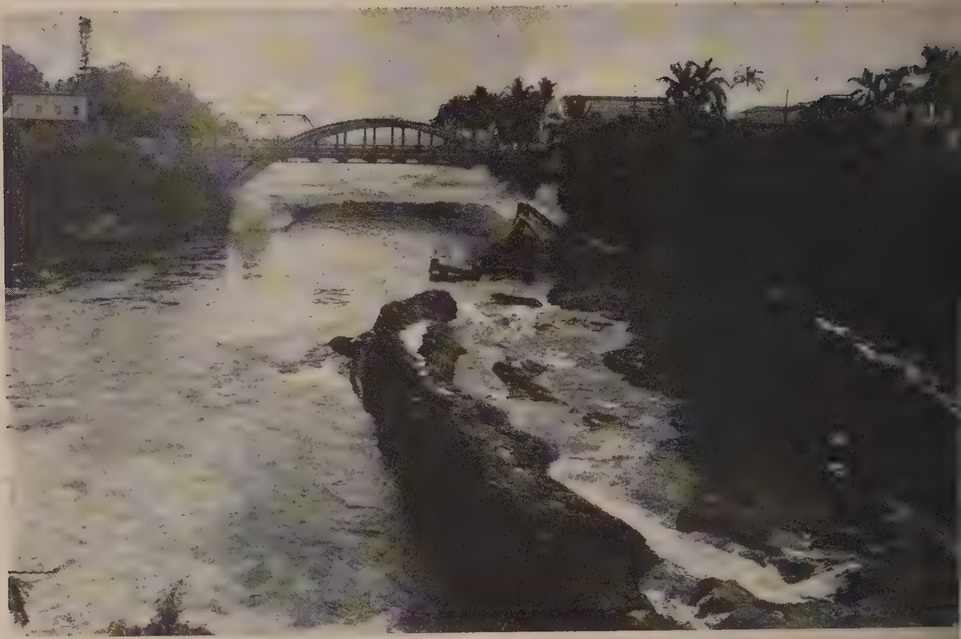


PLATE 4A. Mouth of the Wailuku River at Hilo, showing the advance of one of the later wa
into the river mouth. Photo taken near the trough between two waves, showing very low water, a
the waves starting up the river as the next crest approaches. The steel span from the distant railr
bridge is visible in the middle distance. Photo by Francis Lyman.

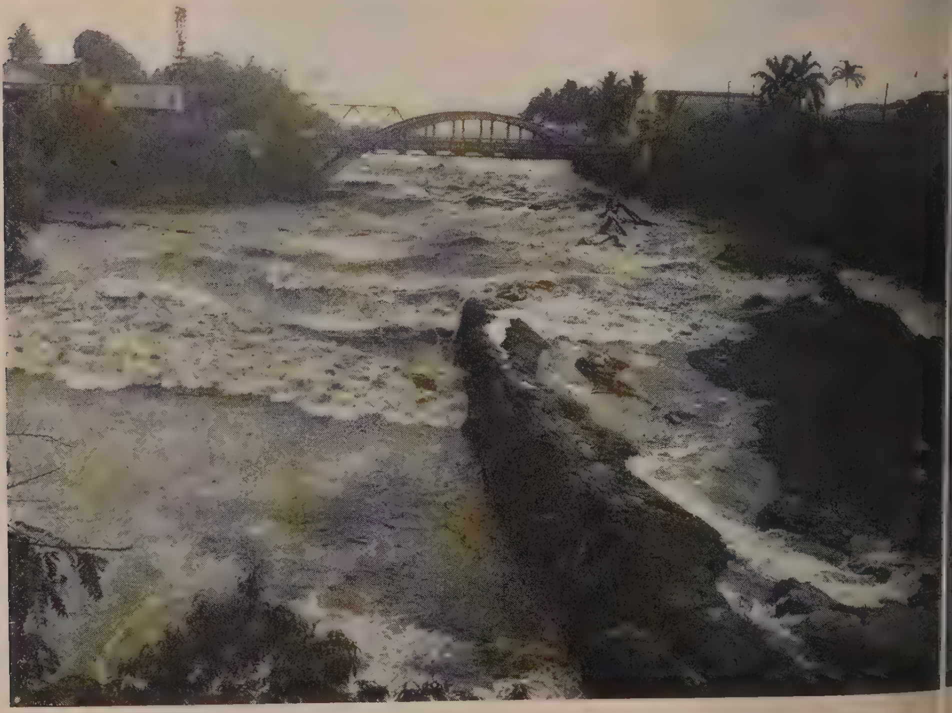
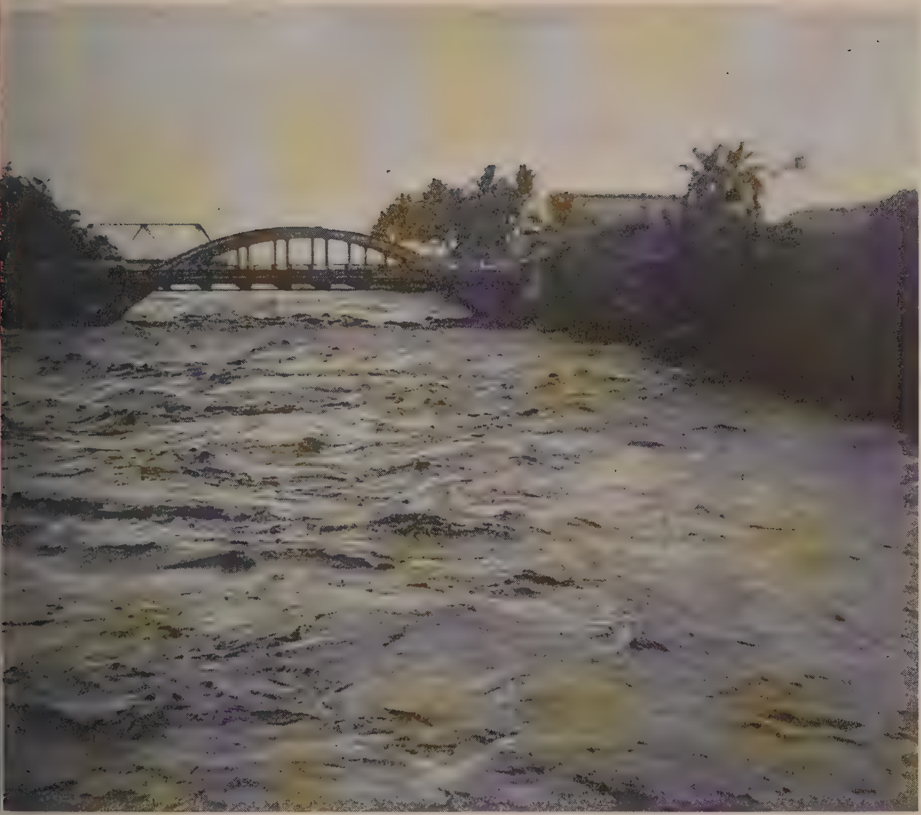
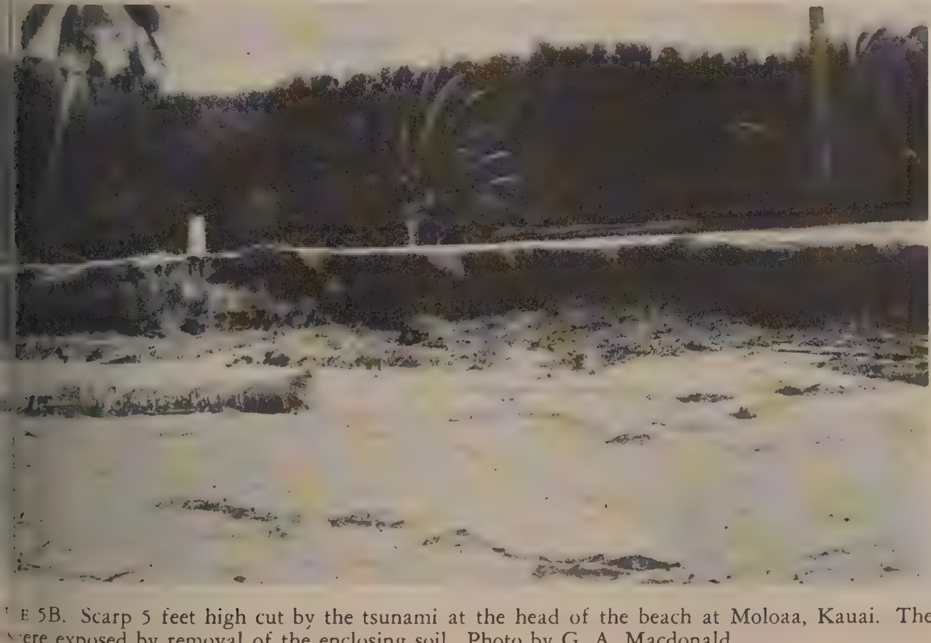


PLATE 4B. A minute or so later, the waves are sweeping turbulently up the river. Photo by F
Lyman.



TE 5A. The very high stage of the water, in Wailuku River at Hilo, reached 3 or 4 minutes
han the stage shown in Plate 4B. Photo by Warren Flagg.



E 5B. Scarp 5 feet high cut by the tsunami at the head of the beach at Moloaa, Kauai. The
ere exposed by removal of the enclosing soil. Photo by G. A. Macdonald.

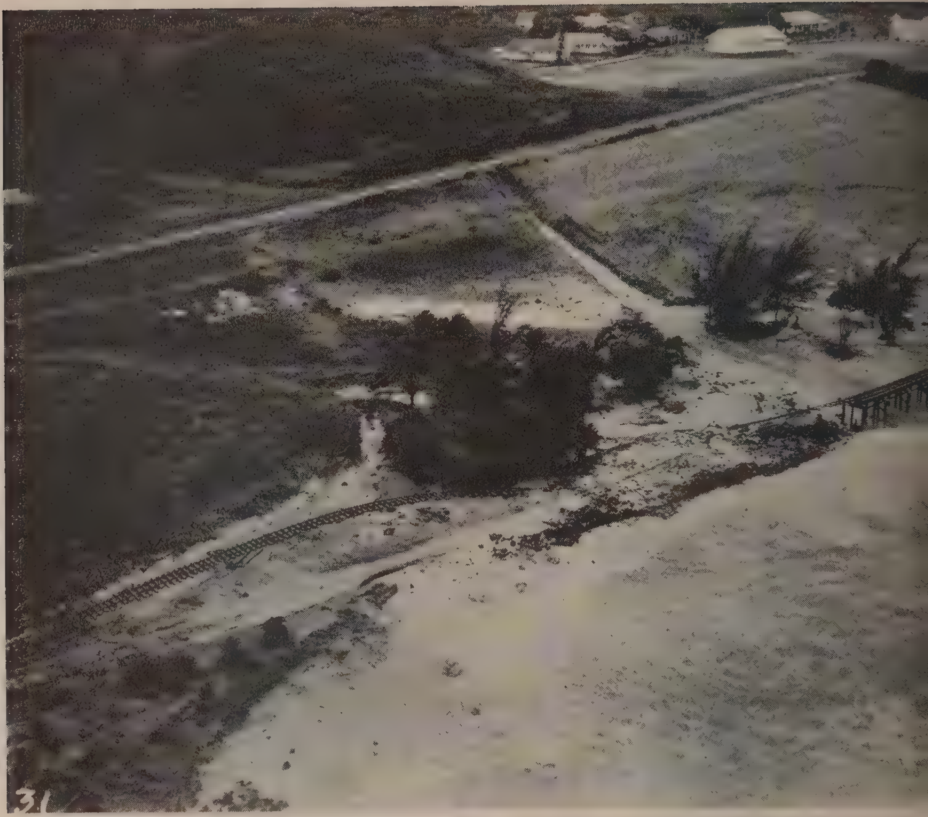
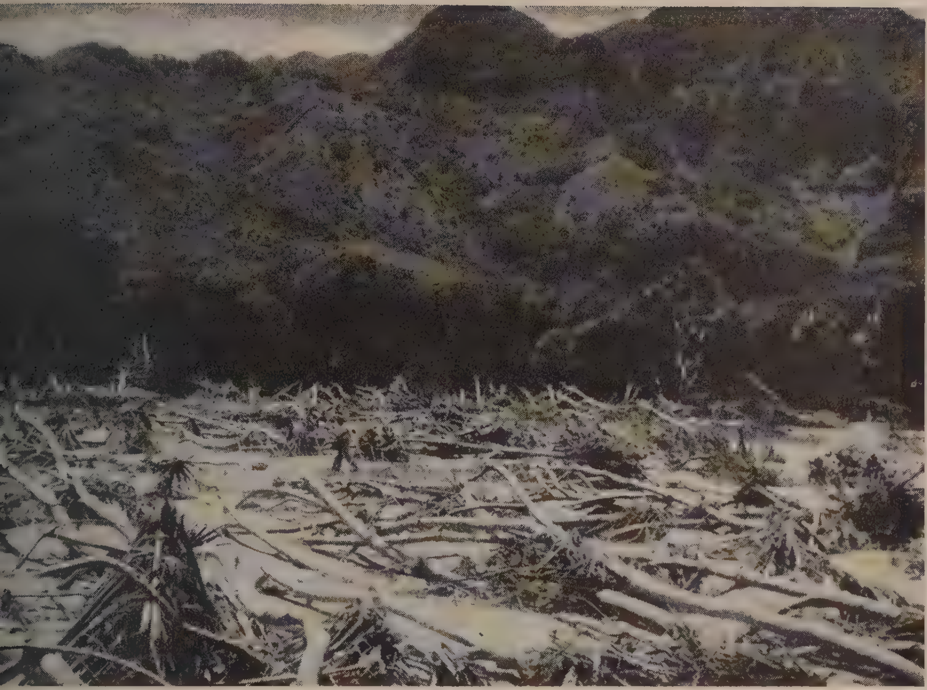
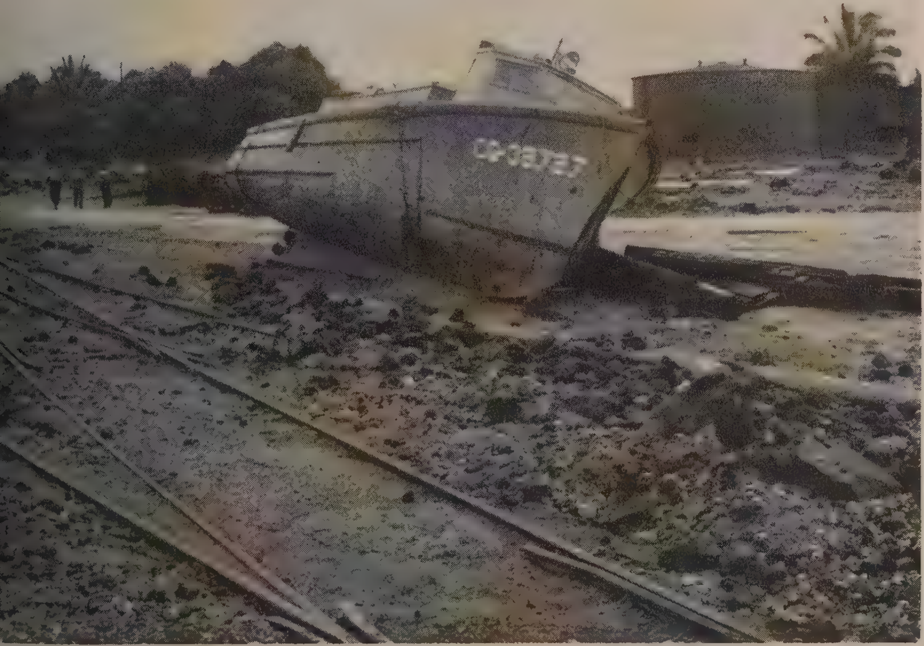


PLATE 6A. Railroad track swept inland from its bed at Waialee, Oahu. Photo by U. S. Navy.

PLATE 6B. Coral heads thrown up on the beach at Kaaawa, Oahu, by the tsunami. Photo by Macdonald.



ATE 7A. Grove of pandanus trees pushed over, and blocks of coral thrown up on the shore plat-
by the tsunami near Haena, Kauai. Photo by F. P. Shepard.



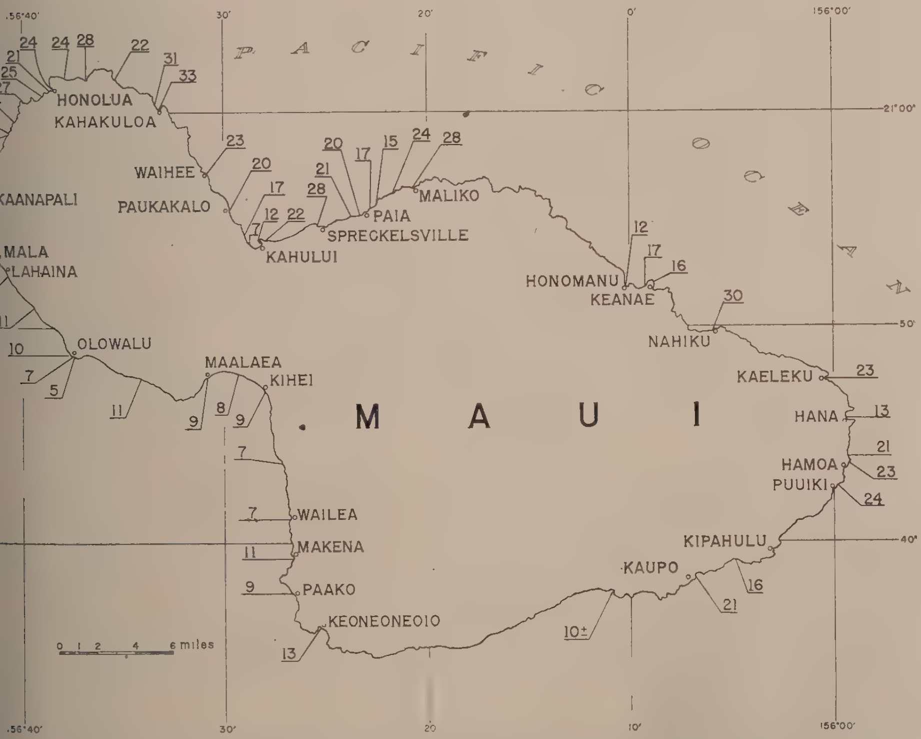
TE 7B. Small boat washed inland and left stranded by the tsunami near Pier 1, Hilo. Photo
A. Macdonald.

on the heights at their heads; but it be noted that they extend across the direction of wave advance, not it.

greater heights reached by the water heads of submarine ridges are not t to explain. The ridge has a greater in limiting the movement of water es in the advancing wave than does eper water alongside it. Consequently rtion of the wave over the ridge is d more than that away from the ridge, e wave front becomes bent, with its ity directed toward the ridge head. sult is a focusing of wave force on the t the head of the ridge (U. S. Navy graphic Office, 1944: 13).

larly, in moving toward shore along s of a submarine valley, the part of the wave in the deep water along the valley axis moves faster than that in shallower water on the two sides. In consequence the wave front becomes bent, with its convexity toward the valley head. In the vicinity of the valley head the force lines (orthogonals) of the wave are diffused or spread apart, and over any unit area the force of the waves striking shore is greatly decreased.

An example of the effect of a submarine valley in lessening the force of the waves at its head is found at Kahana Bay, on Oahu (Fig. 4). There the waves dashed to heights of 11 to 17 feet on the coasts north and south of the bay, but reached heights of only 4 to 7 feet in the bay itself. A small submarine valley extends 2 miles northeastward from the bay, to a depth of 150 feet. An example on a much larger scale is af-


.56°40'
30'
20'
0'
156°00'
21°00'
50'
40'
P A C I F I C O C E A N
HONOLUA
KAHAKULOA
WAIHEE
KAANAPALI
PAUKAKALO
MALIKO
PAIA
SPRECKELSVILLE
KAHULUI
MALA
LAHAINA
HONOMANU
KEANAE
NAHIKU
OLOWALU
MAALAEA
KIHEI
KAELEKU
HANA
HAMOA
PUUIKI
WAILEA
MAKENA
KIPAHULU
KAUPO
PAAKO
KEONEONEOIO
M A U I
0 1 2 4 6 miles
24 24 28 22 31 33 21 25
23 20 17 20 21 17 28 12 22 7 15 24 28
12 17 16 30 23 13 21 23 24
10 7 5 11 9 8 9 7 7 11 9 13 10± 16 21
.56°40'
30'
20
10'
156°00'

5. Map of the island of Maui, showing heights (in feet above lower low water) reached by er during the tsunami of April 1, 1946.

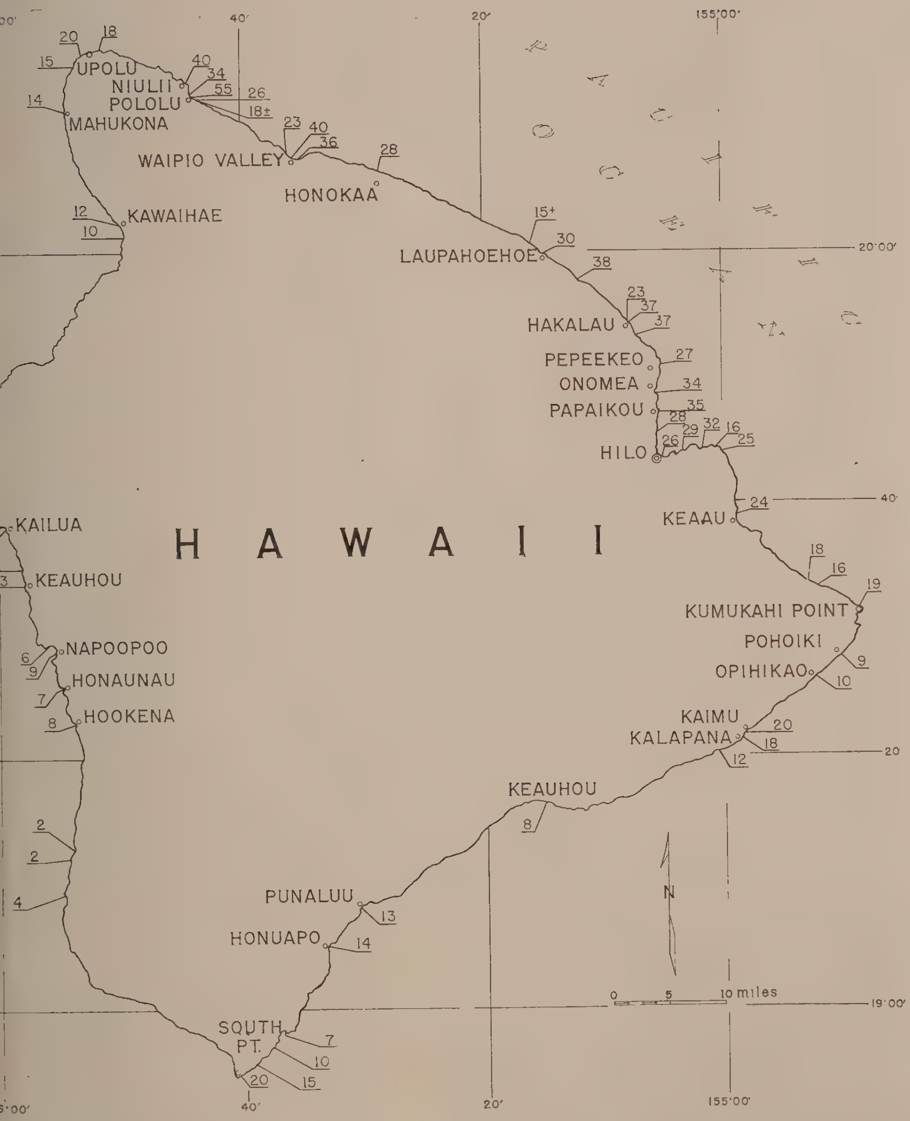
forded by the zone of small heights along the northwestern shore of Kauai (Fig. 3), at the head of a broad swale extending outward to oceanic depths. The broad valley-like depression off the eastern coast of Hawaii south of Hilo Bay probably also was somewhat effective in reducing the heights reached by the water along that coast. Although fairly great, ranging from 16 to 19 feet, the heights there are not much greater than those reached by ordinary storm waves.

Presence or absence of reefs.—The presence of a well-developed fringing reef appears to have had a decided effect in reducing the intensity of wave onslaught. Along the reef-protected northern coast of Oahu the heights reached on shore by the waves were on the average decidedly less than on the unprotected northern coasts of Molokai and Hawaii, or on the less protected northern coast of Kauai. The best-developed coral reef in the Hawaiian Islands fills Kaneohe Bay on Oahu, where it has a width of about 3 miles. Despite the fact that the broad mouth of Kaneohe Bay is open to the north and northeast, the tsunami produced a rise in water level at the bay head which was so small as to be hardly perceptible to observers, and, so far as could be determined, nowhere exceeded 2 feet. Along the shore north of the bay the heights ranged from 4 to 10 feet, and on the end of Mokapu Peninsula southeast of the bay the heights reached more than 20 feet (Fig. 4).

The lesser heights along the southern shore of Molokai were probably partly due to the wide protecting reef. The effect of the reef in reducing wave violence along that shore is well shown at places where channels cross the reef. There the waves striking the shore at the heads of the channels were distinctly larger than those reaching shore on each side of the channel. Thus at the head of a small channel which crosses the reef just west of the mouth of Kainalu Stream the water rose 11 feet, damaging houses, whereas just east and west of this chann
water rose only 7 to 8 feet.

Configuration of the coast line.—It
erally considered that the effects of ts
should be intensified near the heads
shaped embayments. Such embayment
ly increase tidal fluctuations, as in t
of Fundy, and might be expected to a
wise on the similarly long waves
tsunami. Imamura (1937: 125–127
that as such a wave rolls up a V-shap
bayment its height increases in invers
to the width and depth of the bay, ar
examples of such increases in height
waves toward the bay head during Ja
tsunamis. Consequently, special sear
made for this phenomenon in funnel-
bays on Hawaiian shores. No good ex
could be found. Hilo Bay would ap
be an almost ideal site for such fun
but measurements around its shores sh
systematic increase in heights toward i
(Fig. 7 and Plate 1). Similarly there
lack of increase in heights toward th
of the broad V-shaped embayment
northern coast of Maui. Possibly t
treme height of 54 feet at Waikolu
on the northern shore of Molokai, ma
been partly the result of funneling b
Kalaupapa Peninsula and the point and
islands just east of the mouth of the
At both Pololu Valley on Hawaii and
kunu Valley on Molokai, the water lev
higher at the bay head than on the w
the bay part way out. However, at
Valley, and probably also at Pelekun
level was the result of a local upsurge
the waves crossed the beach. Conv
several bays were found in which the h
reached by the water were less at t
head than near its mouth.

Several small steep valleys, debou
into small bays, were found in whi
water rose to appreciably greater h
along the valley axis than on the side
the bay mouth or opposite the beach.



HAWAII
UPOLU
NIULII
POLOLU
MAHUKONA
WAIPIO VALLEY
HONOKAA
KAWAIHAE
LAUPAHOEHOE
HAKALAU
PEPEEKEO
ONOMEA
PAPAIKOU
HILO
KEAAU
KUMUKAHI POINT
POHOIKI
OPIHIKAO
KAIMU
KALAPANA
KEAUHOU
PUNALUU
HONUAPO
SOUTH PT.
KAILUA
KEAUHOU
NAPOOPOO
HONAUNAU
HOOKENA
20
18
15
14
40
34
55
26
18±
23
40
36
28
12
10
15+
30
38
23
37
37
27
34
35
28
29
32
16
25
26
24
18
16
19
9
10
20
18
12
8
13
14
7
10
15
20
3
6
9
7
8
2
2
4
40′
20′
155°00′
20°00′
40′
20
19°00′
N
0
5
10 miles

Map of the island of Hawaii, showing heights (in feet above lower low water) reached by r during the tsunami of April 1, 1946.

in the small bay just south of Hanamaulu Bay, on the eastern shore of Kauai, the water rose only 25 feet on the bay sides, but swept up the small valley at its head to a height of 40 feet. At Moloaa, on Kauai, the water reached an altitude of 40 feet in the axis of the valley, but only 30 to 35 feet on the bay walls. Again, at Honouliwai, on Molokai, the water reached a height of 27 feet opposite the beach, but went 6 feet higher up the valley. These are merely specialized examples of effect, upon the rush of water up on shore, of a topography above sea level which served to concentrate the inrushing water.

Merging of waves from different directions. —Wave crests traveling by different routes may arrive at a given locality simultaneously, giving rise to a wave of greater size than either. Likewise, the simultaneous arrival by different routes of a wave crest and a wave trough may effectually cancel out both. Thus, variations in the size and intensity of waves, particularly on the sides of the islands away from the wave origin, may result from the arrival, either in or out of phase, of two wave trains. During the tsunami of 1946 several examples of the formation of a large wave by the juncture of two smaller ones were observed. Thus, in the Keaukaha area east of Hilo, witnesses described the arrival of a wave from the north simultaneously with one from the northeast, which built up a very high crest at the place of juncture. At the head of Maunalua Bay, on the southeastern shore of Oahu, two waves were seen to advance up channels across the wide reef, move toward each other parallel with the shore, and meet, throwing water upward like the spray from a geyser. The water dashed up on shore to a height of only 3 feet except at the place of juncture, where it swept over the top of a sandspit 5 feet above sea level.

Progressively southward around the shores of Kauai, the average height of the high-water marks gradually decreases, and along much of the southern shore it is 6 to 12 feet above sea level. However, in a zone 3 miles wide it ranges from 15 to 18 feet. zone is almost directly across the island the direction of wave origin, and pro represents the area in which the wave fracted around opposite sides of the i met and reinforced each other.

DAMAGE BY THE TSUNAMI

Damage by the tsunami can be di into structural damage, damage by er and deposition, and damage by flooding. total property damage has been estin by the office of the Governor, Territo Hawaii, at about $25,000,000. Space mits only a brief review of the types of age. The numbers of dwellings destr and damaged by the tsunami on the n islands are listed in Table 2 on page 36.

Structural damage includes damag buildings, roads, railroads, bridges, p breakwaters, fishpond walls, and s Frame buildings at low altitudes a Hawaiian shores suffered extensive age. Some were knocked over, by the f of the waves, by cutting away of the san which they stood, or by destruction of foundations. Others were bodily wa away from their foundations. Some walls pushed in by the force of the w and in a few residences the water wen through the house and took out the opp wall. As with earthquakes, there was a t ency to reduce the few two-story build to a single story, by destruction of the lo story. It is noteworthy that houses w were well built and tied together inter could be moved for considerable dista without suffering severe damage. Even r striking was the fact that houses elevate stilts a foot to several feet above the gro survived the waves much more effecti than did those built directly on the grou Apparently the water was able to pass u such houses without greatly disturbing th unless it was deep enough actually to ouse off the stilts. The few reinforced ete structures in devastated areas suf- little or no damage except that caused oding.

e railroads along the northern coast of and in Hilo were wrecked, partly gh destruction of the roadbed, but y because the tracks were shifted off the ed, either inland or shoreward. Locally were torn loose, but more generally the was moved en masse, a motion probably by the buoyancy of the ties. Coastal vays also were partly destroyed, largely ndercutting as the water returned sea- but partly by the direct force of the . Several highway and railway bridges destroyed. Most appear to have been or entirely lifted from their foundaby the rising of the water under them. ead of the pier at Waianae, Oahu, was ged in the same manner. At the Wai- River, in Hilo, an entire span of the railroad bridge was torn loose and d 750 feet upstream, passing under but amaging a highway bridge. At Kole- tream, 11 miles farther north, an entire the high steel railroad trestle was re- d and carried upstream about 500 feet.

t of the end and much of the shed of in Hilo was wrecked by the force of ave. Most of the damage on Pier 2, ver, resulted when heavy pontoons, had been moored near by, were washed the pier. The wharves at Kahului on were flooded, but sustained little struc- lamage.

upper part of the breakwater at Hilo bout 61 per cent destroyed (Plate 1). of rock weighing more than 8 tons ifted off the breakwater and dropped nside and outside it. Destruction was d, however, to the part above water or nly slightly submerged. The average of water over the destroyed sections he wave was only about 3 feet. The vater at Kahului, Maui, also suffered minor damage. At both Hilo and Kahului the breakwaters appear to have reduced materially the height and violence of the waves in the enclosed portions of the harbors.

Many small boats were washed ashore and damaged. Railroad cars were overturned on Oahu, Maui, and Hawaii. Many automobiles were wrecked. The loose stone walls of fishponds along the southern coast of Molokai were partly thrown down. The mill of the Hakalau Sugar Company, situated only about 10 feet above sea level at the mouth of Hakalau Gulch on the island of Hawaii, suffered severe damage.

Erosion by the tsunami resulted in the partial removal of some sand beaches, in some places causing a retreat of the shore line for several tens of feet, cutting of small scarps, and forming of large beach cusps at the heads of beaches; locally, erosion caused stripping away of a small amount of soil. The erosion was largely concentrated high on the beach, several feet above sea level. Some of the sand from the beaches was carried inland and redeposited. At Haena, Kauai, the highway was buried under 4 feet of sand, and thinner layers of sand covered roads on Oahu.

Flooding caused much water damage to house furnishings and personal property.

LOSS OF LIFE AND PERSONAL INJURY

The following table summarizes, by islands, the number of persons killed, injured, or missing as a result of the tsunami. The figures were supplied by the American Red Cross. Most of the deaths were by drowning. By far the heaviest toll was at Hilo, with 83 known dead and 13 missing. Those listed as missing have been missing for more than 2 months, and must be presumed dead, bringing the total number of probable dead to 159. Great as it was, this loss of life was moderate compared to that in some other tsunamis, such as that of 1896 in the Sanriku district in Japan, which took more than 27,000 lives (Byerly, 1942: 72).

TABLE 2

LIST OF CASUALTIES DURING THE TSUNAMI OF APRIL 1, 1946

ISLAND	KNOWN DEAD	MISSING	INJURED*	HOMES DEMOLISHED†	HOMES DAMAGED†
Hawaii	87	34	153	283	313
Maui	9	5	2	65	144
Oahu	9	0	0	67	335
Molokai	0	0	0	13	14
Kauai	10	5	8	60	130
Total	115	44	163	488	936
	159				

* Injury sufficiently serious to require hospitalization.
† Homes only; other buildings not included. Data from Lewers and Cooke, Ltd.

MITIGATION OF DISASTERS RESULTING FROM FUTURE TSUNAMIS

There is no Hawaiian shore which is exempt from tsunamis. The most likely sources of devastating tsunamis are the North Pacific and South America. The areas heavily hit by the 1946 tsunami are probably those most likely to be hit hard again by tsunamis from the North Pacific. Violent tsunamis from Central or South America might, however, cause much more damage than did the 1946 tsunami along eastern and southern coasts. There is also possibility of serious damage on western shores by a tsunami from Japan, particularly if the tsunami occurred during a heavy southwesterly storm. Tsunamis of local origin might do heavy damage on any shore.

It is obviously impractical to consider the removal of all dwellings from Hawaiian shores because of the danger from tsunamis. It might, however, be advisable to prevent or restrict building in certain areas of greatest danger, particularly in centers of heavy population, such as the waterfront at Hilo. Construction of suitable sea walls might also be advisable in places. Sea walls cannot, however, be built high and strong enough to hold the water back completely, and an op
should be left back of the wall in wh
water pouring over the wall can use
energy in turbulence. Any constructi
mitted in such areas should be of a
resistant type, such as reinforced c
These wave-resistant buildings woul
the added virtue of serving as a line
fense for frailer structures behind
Frame structures in rural areas sho
built up off the ground, and far enou
from the edge of the beach to red
danger of undercutting. They should
properly reinforced and tied together

It appears inevitable that future ts
will cause loss of property on Ha
shores, but loss of life from all exce
namis of local origin could be largely
tirely avoided. A system of stations c
established around the shores of the
and on mid-Pacific islands, which wo
serve either visually or instrumenta
arrival of large long waves of the
characterizing tsunamis. The arrival c
waves should be reported immediate
central station, whose duty it would
correlate the reports and issue warni
places in the path of the waves. It sho
possible in this way to give the people
Hawaiian Islands enough warning of
proach of a tsunami to permit them t
places of safety. The effectiveness
warning, however, would depend on
tion of the public on the necessity for
areas of danger, and on the efficiency
local organization in spreading the w
and evacuating the threatened areas.
ually it should also be possible to state
same time, which areas are likely to su
most damage. Before that can be done
ever, we need more knowledge of t
havior of tsunamis on Hawaiian shore
ticularly tsunamis from sources in th
ern and western Pacific, and a more co
picture of the submarine topography
the Hawaiian Islands.

SUMMARY

tsunami which reached the shores of waiian Islands on April 1, 1946, was st destructive in the history of the Generated by a sudden shifting of bottom on the northern slope of the n trough, the waves traveled south- Hawaii with an average speed of 490 n hour, an average wave length of 22 miles, and a height over the deep f about 2 feet. Effects on Hawaiian varied greatly. Locally the water more than 50 feet above sea level and s much as half a mile inland. Else- he rise in water level was very small, es were gentle. Property damage was ut loss of life was moderate.

ieights and intensities of the waves at t points were influenced by position sland toward or away from the source aves, offshore submarine topography, e or absence of coral reefs, shore-line ation, mutual reinforcement or inter- by waves traveling different paths, presence or absence of storm waves. property during future tsunamis can ced by proper construction, by erec- sea walls, and by restricting or prohibiting construction in certain especially dangerous areas. Loss of life can be nearly or entirely eliminated by the establishment of a suitable system for warning of the approach of waves.

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Contribution No. 321

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Breeding Behavior and Early Development of the Mudsucker, a Gobiid Fish of California[1]

By GEORGE F. WEISEL, JR.

ONE of the most remarkable fishes of the Californian fauna is the mudsucker or long-jawed goby, *Gillichthys mirabilis* Cooper. Rather large or a goby, it reaches a length of at least 8 inches. It is common in the bays nd estuaries of southern California and northwestern Baja California. It as been reported from as far north as Puget Sound (Jordan and Starks, 895: 839). Records from the Gulf of California, as that of Evermann and enkins (1891: 162) from Guaymas, were based on related species, *Gilichthys detrusus* Gilbert and Scofield and *G. seta* (Ginsburg).

The mudsucker is the chief bait fish of southern California. It is reported hat many thousands per week are harvested and sold. Its popularity is ttributable not only to its suitable size and extreme hardiness but also to its bility to survive for several days in fresh water. Consequently, it is widely used for fishing in lakes as well as in the bays and seas. Its inability to ropagate in fresh water renders it a safe fish to use as bait.

Little has been published concerning the life history of *Gillichthys mirailis*, and part of the little that has been written is of doubtful validity. Eigenmann (1892: 159, pl. 15, fig. 12) figured the young, which is remarkbly unlike the adult, and stated that the species begins to spawn in the San Diego area about the end of March, at which time it ceases to feed and retires o crab holes. Actually it spawns as early as January and appears to move bout at night during all seasons. Hubbs (1921: 1–3) described the young as a distinct genus and species, *Aprolepis barbarae*, but later (1926: 3) corected the error. Barnhart's statement (1936: 82) that it is most abundant n sloughs, and hides in the holes of the mud banks is true, but his indication hat it hibernates in winter is not confirmed. Young and Fox (1937: 1) ound many males with motile sperm and females with enlarged ovaries in May and June. Observations by bait dealers and by me confirm this finding and show that a few females mature as late as July.

The breeding behavior of the mudsucker has not been described. Some bait dealers have attempted the artificial propagation of this fish but report ack of success. Though it has been exhibited for long periods in the public aquaria of the Scripps Institution of Oceanography and at Steinhart Aquarium in San Francisco, no one has seen it spawning. The spawning of a pair in a laboratory aquarium at Scripps Institution was therefore observed with much interest. This observation prompted the preparation of this paper.

BREEDING BEHAVIOR

On January 1, 1946, several adults of *Gillichthys* were procured for experimental purposes from a bait dealer in San Diego. They were placed in 20-gallon stock tanks with a thin bottom layer of fine gravel. Nest building activities were first noticed in the middle of January. Closer observations revealed that a large goby had established territory in the most secluded

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[1] Contributions from the Scripps Institution of Oceanography, New Series No. 321. Acknowledgment is due to Dr. Carl L. Hubbs and his students for their aid in collecting material, and again to Dr. Hubbs for suggesting the problem and for his critical reading of the manuscript.

corner of a tank and was constructing a nest. He regularly drove his twel
tank companions away from this area by biting them on the head and alo
the sides. In a week's time the chased fish were content to take residence
the previously avoided parts of the tank where they were most subject to di
turbance by passers-by.

In the construction of the redd, a square foot of crushed gravel abo
1½ inches deep was cleared from the bottom of the aquarium. The ta
took a full two weeks of intermittent labor. Most of the gravel was mov
by either a fanning motion of the tail or by a quick rolling of the body. N
infrequently the nest builder carried gravel in his mouth to the opposite e
of the tank.

On several occasions a startling display of combat was exhibited. Th
took place whenever a large male ventured into the nesting territory of t
established male. The first sign of approaching battle was the rigid expansi
of dorsal and anal fins. In a few seconds the anal and pelvic fins were su
fused with sooty-black. This color appeared later on the dorsals and then e
tended as a less intense darkening over the entire body. The defender w
first to present the next and most frightening battle array. He opened h
mouth to its fullest extent, which in *Gillichthys* presents a huge gape a
spreads the maxillaries out at right angles to the body (Fig. 1). In this pos
the membrane between the maxillaries and dentaries stretches sail-like
either side of the mouth. The adversary followed example and the tw
squared off, pushing against each other jaw-to-jaw. This was repeated two
five times, and twice in six trials the guardian pushed the intruder back t
full length of the tank, 2½ feet. The battles terminated when the intrud
retired to the end of the aquarium farthest from the redd.

Incidentally, it may be mentioned that the rich vascularization of t
jaw membranes (Fig. 1) leads one to suspect that they serve as an accesso
respiratory apparatus. Such additional respiratory devices are not unco
mon among the gobies. *Typhlogobius* has subepidermal blood vessels (Ritte
1893: 90–93), *Perioptha lmus* a modified caudal (Hickson, 1889: 30–31
and *Bathygobius* modified pectorals (Beebe, 1931: 63–65) for use in respir
tion. However, adult mudsuckers did not gape when kept in a sealed vess
of water until they nearly suffocated.

The breeding color is transitory and disappears as quickly as it appear
This rapid color change has been noticed in *Gobiosoma robustum* by Bred
(1942: 62) and in *Bathygobius soporator* by Beebe (1931: 61–63). T
courtship hues of *Gillichthys* are not confined to the males, nor is the ja
spreading and pushing. Mature females were frequently seen to assume t
black coloration and also to push off males and other females that happen
to swim into their acquired area. Neither the pushing nor the color chan
occurred among the smaller gobies. Nor did it take place other than in t
spawning season.

The sexual dimorphism in this species is slight. In the aquarium the m
ture sexes may be distinguished only by close inspection. The broad a
swollen genital papilla of the female contrasts with the more pointed papil
of the male. The abdomen of the ripe female is fuller and has a yellowis
tinge due to the underlying ova. Less obvious differences are the blunt

ıose of the male and the slightly greater width of the maxillary tip. There are ıo patterns or general coloration which can be used for a definite separation ıf the sexes.

On February 5, I removed all fish with the exception of the nest guardian ınd what was obviously his chosen mate. She had often been seen by his ide in the nest, whereas any other fish was immediately driven off. Remainıng calmly in their secluded corner, the pair exhibited little activity. The emale often clung with her pelvic fins to the side of the aquarium.

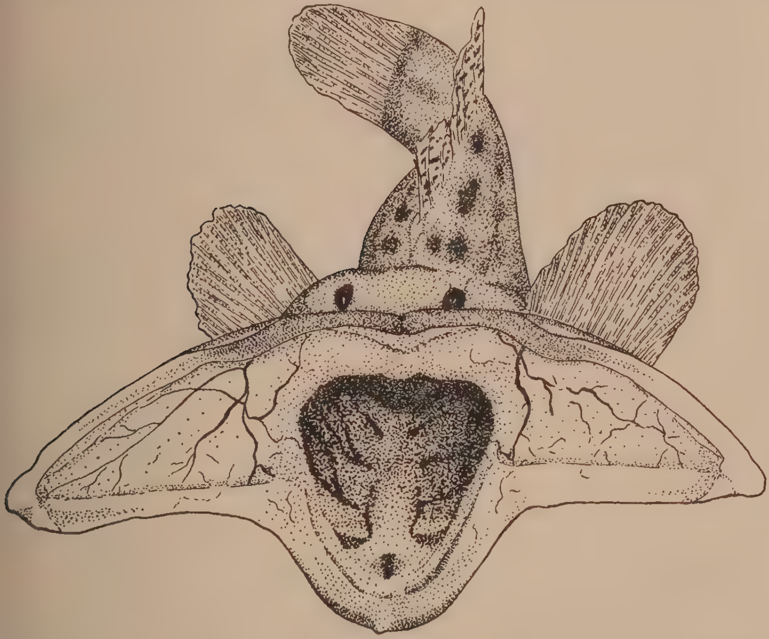

Fig. 1. Adult *Gillichthys mirabilis* in combat pose. Drawn from photograph by aul Williams.

The pair spawned, unobserved, during the night of February 6–7. In he morning several masses of eggs adhered to the glass walls in the nesting orner. The male lay as close as possible to the eggs. When tickled with a od, he refused to budge from his place of guard. No fanning of the eggs /as noticed. The female was at the end of the tank away from the nest. Vhen driven into the nest, she was ignored by the male.

The egg masses adhered loosely to the glass. They were placed as far up s 6 inches from the bottom of the tank, which would indicate that the emale must have pressed herself against the side in a vertical position during he extrusion of her eggs. Most of the eggs were in two large clusters. There /ere six separate groups of from four to twenty eggs close to the two large ıasses. Very few eggs were on the floor of the redd. One of the larger aggreations of eggs was removed twice during the day and studied under a microcope.

The male remained alongside the eggs all day. The female exhibited only indifference. In contrast with the usual voracious habits of the species, neither of the pair ate for several days after the spawning. Nor had they shown interest in food for two days previous to the act.

The morning following these observations, we were disappointed to find that most of the eggs had been eaten. Only a couple dozen scattered eggs remained. These were carefully removed and placed in a glass container. They provided the material for the following descriptions of all egg stages, except the earliest.

Eggs and Embryos

The eggs are laid in large clusters which to the unaided eye resemble hundreds of minute yellow grapes on a stem. Their specific gravity is but slightly greater than that of sea water. It was estimated that 4,000 eggs were laid by the one spawning female. Nearly all of the eggs were fertile. A gravimetric count of eggs removed from three other mature female ranges from 4,000 to 9,000, varying with the size of the fish.

Under magnification, the few unfertilized eggs included in the spawned mass are spherical. The yolk mass nearly fills the egg (Fig. 4). Six of these eggs measured 1.03 to 1.18 mm. in their greatest diameter. At one pole of the egg is an interwoven group of adhesive threads. Directly after fertilization the vitelline membrane expands and the egg assumes its typical elliptical shape.

The fertilized egg is shaped like an Indian club. Its round yellow yolk mass is usually situated toward the large end of the club. There is a wide hyaline perivitelline space. The opaque yolk, which occupies only about one-third of the area within the vitelline membrane, has many oil globules. Numerous adhesive threads are bunched at the narrow pole of the long axis. These threads entwine about a central stalk from which the eggs dangle in clusters (Fig. 5). The major axis of the fertilized egg is 2.77 to 3.37 mm. and the minor axis 1.06 to 1.13 mm. The yolk diameter varies from .75 to .87 mm.

On the first day after fertilization a rounded blastoderm fits like a cap over the yolk (Fig. 6). The blastoderm is directed toward the attached pole in 95 of 100 examples studied. The remainder have the cap toward the unattached end. Twenty-four hours later the blastoderm has grown around the egg and there is a well developed primitive streak with an anterior swelling, the anlage of the embryonic head (Fig. 7). Many fine, relatively short gelatinous threads cover the surface of the membrane at this stage and those that follow. These threads do not entwine and adhere to one-another as do those at the attached end. They were not noticed previous to this time, and a re-examination of some preserved earlier stages did not reveal them. Literature and illustrations of American gobies which were reviewed gave no intimation that threads other than at the pole of attachment were present on the eggs of related species.

By the third day of development the embryo has definite outlines. The eye is forming and the embryo is much less opaque than the yolk. On the fourth day there are ten to fifteen somites (Fig. 8). As differentiation continues, the yolk becomes smaller and the number of oil globules is reduced. The embryo becomes progressively more transparent but the yolk remains paque. Most of the embryos are so situated that the head is directed toward the pole opposite from the attached end. This polarity was noticed in *Bathygobius soporator* by Breder (1943: 6) and an opposite polarity in *Gobiosoma bosc* by Hildebrand and Cable. Measurements of the egg's longst axis taken twice daily showed no elongation takes place after the initial engthening that follows fertilization. The major axis remains approximately 3.23 mm.

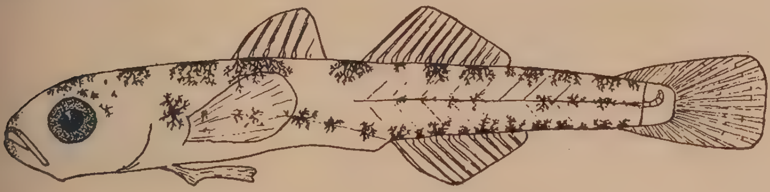

Fig. 2. Postlarva 11.5 mm. in total length.

Movement of the embryo is evident on the fifth day. Most of the features f the six-day embryo (Fig. 9) are now evident. The fin folds contrast with he rest of the embryo by reason of their greater transparency. The posterior ut, the auditory vesicles, and the vertebrae are differentiating. By the sixth ay the embryo nearly fills the space within the membrane. The embryonic sh are now 2.54 to 2.65 mm. long. The shape of the vitelline membrane as not changed since the first day. It is apparent that it anticipates the hape of the embryo in its later stages.

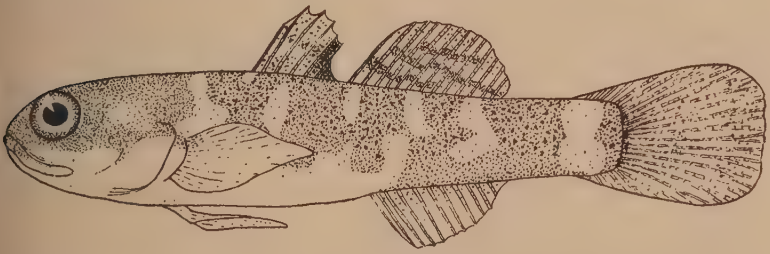

Fig. 3. Juvenile 35 mm. in total length.

On the eighth day many of the embryos have become slightly longer han their surrounding membrane so they must curve the tip of the tail. An r-bladder is distinguishable just above the yolk. The heart has comenced to beat. The eye has become pigmented and melanophores are present along the posterior half of the ventral and dorsal body margins, but not n the fin fold (Fig. 10).

It was expected that the eggs would hatch within the next 48 hours but this critical period the embryos died. The eggs had been kept at an average mperature of 18° C. At this temperature it is safe to assume that the eriod of development prior to hatching is 10 to 12 days.

Young

Young of *Gillichthys* were collected in the sloughs of Mission Bay, San Diego. The smallest (Fig. 2), 11.5 mm. in total length, has the yolk sac absorbed. The chromatophore pattern is much the same as that of the eight-day embryo. There are large stellate melanophores along the mid-dorsal and ventral lines. Just anterior to the anal fin, the ventral melanophores leave the mid-line and extend dorsally in a sloping row to the dorsal base of the pectorals. There are a few melanophores on the posterior part of the lateral mid-line and a number of smaller melanophores about the muzzle and above the eye.

At this and at somewhat more advanced stages the young of *Gillichthys mirabilis* look strikingly different from the adult. They are small-mouthed and large-eyed, whereas the adults have inordinately long jaws and very small eyes. The coloration is also different. Such young were figured by Eigenmann (1892: pl. 15, fig. 12) and were described by Hubbs (1921: 1–3) as *Aprolepis barbarae*. The young figured by Eigenmann is intermediate between my Figures 2 and 3.

Larger juveniles (Fig. 3) develop the typical mottled design of the adult. A characteristic color pattern of the young is the dark blotch on the posterior portion of the first dorsal fin. The maxillaries commence to elongate directly after hatching. By the time the fish are 35 mm. long the upper jaw extends to the posterior margin of the eye. In some of the larger fish, 18 to 20 cm., the maxillaries extend to the base of the pectorals.

Spawning Period

To obtain data on the natural time for the spawning of *Gillichthys*, we started netting for the young in San Diego River and Mission Bay. Also, for examination of their gonads, adults were brought from bait dealers at two-week intervals, from the last of February to the middle of July.

Table I

Size Frequencies of Young of *Gillichthys mirabilis* Seined in 1946 in San Diego River and Mission Bay, California

Date of Collection	Size Groups in Millimeters										
	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60
February 28	...	6	12	1	...	...	...	...	...	...	...
March 2	...	3	1	2	...	...	...	...	...	...	...
April 6	...	1	35	22	38	15	3	...	...	...	...
April 21	1	42	40	151	245	143	6	5	4	1	...
May 5	1	1	1	1	3	40	45	15	8	4	1
May 18	...	...	...	2	...	...	1	...	...	2	1
June 20	...	...	...	...	...	...	...	...	...	...	...

Young were caught each time, but newly hatched juveniles were taken only from February to the last of May. Size frequency distribution of the young (Table I) indicates that the heaviest spawning took place in February, March and April. Since juveniles up to 25 mm. long were netted on the

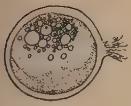

FIG. 4

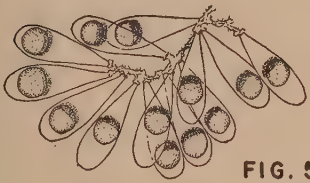

FIG. 5

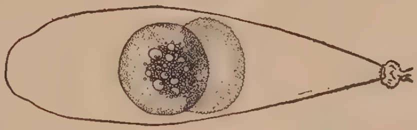

FIG. 6

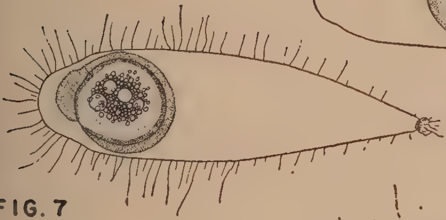

FIG. 7

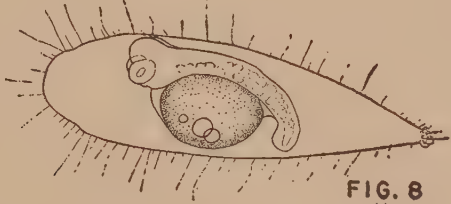

FIG. 8

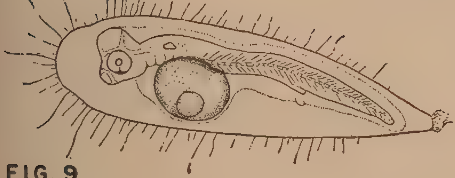

FIG. 9

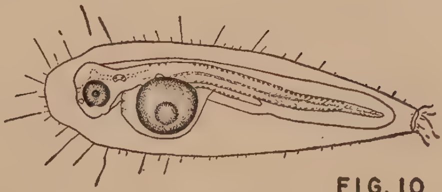

FIG. 10

Figs. 4–10. Eggs and embryos of *Gillichthys mirabilis*

Fig. 4. Mature unfertilized egg. Fig. 5. Portion of the egg mass showing the attachment by lhesive threads. Fig. 6. First day of development. The blastoderm forms a cap over the yolk ward the attached pole. Fig. 7. Second day of development. The anlage of the head forms a swelıg opposite to the attached pole. Fig. 8. Four-day embryo. Fig. 9. Six-day embryo. Auditory placode ıparent above the anterior portion of the yolk. Fig. 10. Eight-day embryo. The air-bladder lies just ıove the yolk sac. Chromatophores are developed and the eye is pigmented.

rst collection, on February 28, spawning must have commenced somewhat ırlier, probably in January.

The condition of the ovaries of adult females procured during the same months conforms fairly well with the data obtained from examination of the young. For February and March, one female in five had spawned, two had mature ova and two immature ova. In April half had spawned, and by June six in seven were through spawning. All but a very few examined in July had depleted ovaries. Since the visible eggs in the ovaries are of equal maturity it is probable that there is a single annual spawning or, under favorable conditions, possibly more than one spawning in the year but some months apart.

SUMMARY

The mudsucker or long-jawed goby is one of the most important baits used for fresh and salt water sports fishing in southern California. Its life history has not been previously described.

A male established territory in a corner of a laboratory aquarium and constructed a redd in the gravel bottom. Intruders into his portion of the tank were driven off with an unusual combative display. The defender and the intruder rapidly darkened in color and then approached one another until they brought into contact their huge jaws, which were extended at right angles to the body. After one or more such performances, during which the defender pushed the intruder away, the latter deserted the nest area. The male selected a mate and the pair spawned.

The fertilized eggs are club-shaped with adhesive threads on one end. They are laid in large masses which resemble hundreds of minute yellow grapes on a stem. The period of development is from 10 to 12 days. The young of *Gillichthys* are unlike the adults in appearance. They are differently pigmented and are small-mouthed and large-eyed, whereas the adults have very long jaws and small eyes.

The spawning period in the San Diego area (determined from collected young and examination of adult gonads) extends from January to July with the height of spawning in February, March and April.

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CRIPPS INSTITUTION OF OCEANOGRAPHY, LA JOLLA, CALIFORNIA.

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BIOLOGY OF CREPIDULA WILLIAMSI, A NEW SPECIES OF PROSOBRANCH GASTROPOD FROM THE PACIFIC COAST[1]

WESLEY R. COE
Osborn Zoological Laboratory, Yale University, and Scripps Institution of Oceanography, University of California

EIGHT FIGURES

At least 2 species of the genus *Crepidula* (*C. nummaria* Gould and *C. nivea* Adams) with flat, white shells are found on the coast of California. These are often designated as belonging to the subgenus *Ianacus*. Both of them are highly variable in size and shape in conformity with the substrates to which they are attached. Consequently some of these growth forms have been given specific, subspecific, or varietal names, rendering the synonymy of the group extremely confusing and the identification of some of the shells difficult (Smith, '46). It has been shown experimentally that when young of the slender dwarf form of *C. nivea* are cultured under suitable conditions they assume a broad oval shape and grow to a size many times greater than would have been possible in their former surroundings. The broad form, rugosa, is similarly assumed by young of the slender form of *C. onyx* Sowerby (Coe, '42a). In that paper, following common usage, the name *C. nummaria* was used for the species now understood to be *C. nivea*.

The new species described in this paper also has a flat, white shell but the apex is marked with a series of radiating lines of dark pigment by which the species can be readily recognized (figs. A, 4, 5, 6). The apical markings are usually sharply demarcated from the remainder of the shell, which is pure white with faintly indicated lines of growth. Although the shell may reach a length of 18 mm or more, the pigmented portion extends for only about 2.0 to 3.3 mm from the apex. This indicates that the snail incorporates pigment in its shell only when it is very young, the production of pigment ceasing at the onset of sexual maturity in the male phase. Only pure white and somewhat translucent shell is deposited during the remainder of the individual's life (figs. A, 4, 5, 6). In some specimens the markings are less distinct and occasionally a few small pigment dots are scattered over the entire shell.

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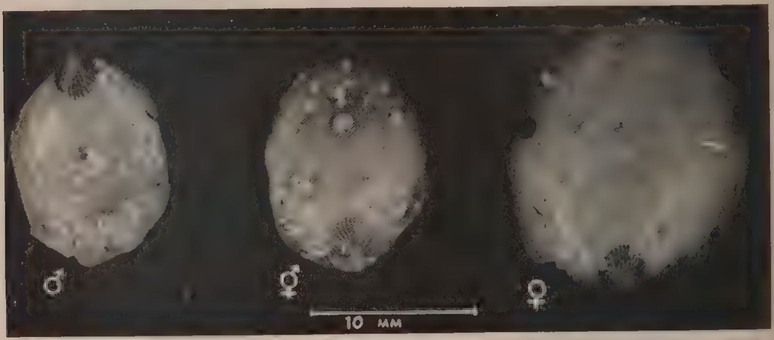

Fig. A Photographs of male-phase, transition, and female-phase shells from dorsal surface. Note that the shell of female-phase is free of worm tubes on right side; in life this side was covered by male-phase individual.

It may be recalled that in all the known species of the family Calyptraeidae, of which *Crepidula* is a member, it is probable that all individuals normally function as males when young and later pass through a transition phase of secondary sexual immaturity and then change to the female phase. The female phase is retained for the remainder of life, often for several years. The male phase is characterized by a large copulatory organ, phallus (fig. 1), by means of which the spermatozoa are transferred to the sperm receptacles of one or more individuals in the female phase.

On completion of the male phase, the production of spermatozoa and spermatosomes in the primarily ambisexual gonad ceases and the growth of the preformed ovocytes is accelerated. During this period the phallus is gradually absorbed, being represented in the late transition phase by a small knob only (fig. 2), and this is almost obliterated in the female phase (fig. 3). During the transition phase the spermary, sperm vesicles, sperm duct and sperm groove are dedifferentiated and the remaining spermatic cells are absorbed. These male organs are then replaced by the ovary, oviduct, sperm receptacles, uterus and vagina of the functional female phase.

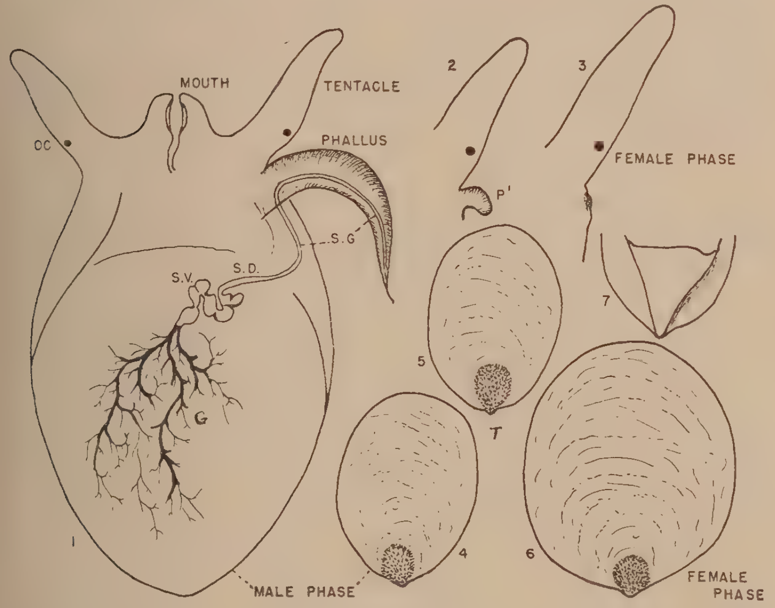

Fig. 1 Reproductive organs of male-phase individual, showing functional phallus with sperm groove (sg), profusely branching gonad (G) leading to sperm vesicles (sv) and sperm duct (sd). Ocellus (oc) near base of tentacle.

Fig. 2 Tentacle and remaining portion of phallus (P′) of individual in transition phase.

Fig. 3 Tentacle and vestige of phallus in female phase.

Fig. 4 Outline of shell of individual in functional male phase.

Fig. 5 Shell of individual in transition phase.

Fig. 6 Shell of individual in female phase. Holotype.

Fig. 7 Portion of ventral surface of shell, showing notch at left edge of septum.

The sexual instincts likewise change and the individual which had been so characteristically male earlier in life now receives her mate, deposits her eggs beneath her foot and broods her young in typically female manner.

It has been shown for other species (Coe, '38) that male-phase individuals which have opportunities for copulation retain that phase longer and consequently reach a larger size before changing to the female phase than those which are isolated. However, the conclusion often seen in textbooks and elsewhere that the association of a young individual with one of larger size, particularly one in the female phase, is necessary for the functional development of the male phase has not been supported by the more recent experimental evidence (Coe, '38a).

In a mated male-phase individual of this new species, that phase was still functional when the shell had reached a length of 14 mm but isolated individuals had begun the transition phase when only 8 mm long and hence less than half the length of the largest female-phase individual. In *C. plana* Say of the Atlantic coast and *C. nivea* Adams of the Pacific coast, both of which closely resemble *C. williamsi* in general appearance and in habit, the transformation from male to female phase likewise often occurs in isolated individuals when the shell is less than half the length that it commonly reaches during the female phase.

Individuals of this and other species of the genus are strictly sedentary after reaching the female phase and depend upon the motility of younger, male-phase individuals for the spermatozoa which they store in their sperm receptacles until their eggs are ready for fertilization. In one species, *C. onyx* Sowerby, the sperm have been proved to remain functional for at least a year after the last copulation (Coe, '42). It has been proved experimentally for other species of the genus that this process of sexual metamorphosis can be modified by environmental influences. It can be accelerated, postponed or inhibited but the sequence of sexual phases cannot be reversed.

In certain species, some of the male-phase individuals after having attached themselves in mating position on the shells of others in the female phase retain that position even after their own transformation to the female phase. Groups of several to a dozen or more superimposed individuals may thereby become established. In other species the male-phase individuals remain in the vicinity of the female and move to the mating position at intervals (Coe, '38).

The fertilized eggs are deposited in gelatinous capsules and incubated beneath the body of the parent. After completing development to the adult form, the juvenile snails move about freely for a time and then attach themselves to some solid object, frequently to the shells of larger individuals of the same species. The size and shape of the object influences the size and shape of the adult shell, since the motile young seldom move far from their birthplace and the shell cannot greatly exceed in size the object to which the foot of the animal is attached. Otherwise the naked part of the body would be exposed to the attacks of enemies. An isolated individual will consequently remain sterile in the female phase unless a young individual settles on her shell, or so near that he can move to the mating position. When attached to the inside of the aperture of an empty gastropod shell or one that is occupied by a hermit crab, as is usual in *C. williamsi*, the shell of the Crepidula is very flat and smooth but if attached to the outside or to a stone, it is less flattened and may have a more irregular surface.

Crepidulas are mainly plankton- and detritus-feeders throughout life, ingesting, together with much inert material, only minute organisms and organic particles. These are collected from the water passing over the gill, and imbedded in sheets or strands of mucus. The mucous strands containing the food particles are then carried by ciliary action through a long food groove on the dorsal surface of the body and thence to the mouth. In the motile juvenile and male phases additional food is secured by browsing, whereby unicellular animals and minute algae may be obtained. In these young phases the radula with its many teeth is doubtless more essential than in older individuals.

Specific diagnosis. Shell usually extremely flat and thin, oval or rounded in outline; juvenile shell, which is retained at apex of adult shell, marked by about 15 to 20 radiating, irregular and interrupted rows or lines of reddish brown pigment spots; pigmented area ceases abruptly after the shell reaches a few millimeters in length, the additional growth being pure white and somewhat translucent, without periostracum, faintly marked with growth lines but without longitudinal striations; apex on margin, nearly symmetrical but turned slightly toward the right; ventral surface porcelaneous white except for faint tinge of reddish near margin of horizontal septum in some specimens; septum with delicate transverse striations only; free edge of septum nearly straight except for broad, shallow, U-shaped notch near left end (fig. 7); body and foot in life pale yellowish or straw-colored, with a distinct rosy tinge in area between head and attachment of body to septum. Occasionally the apical markings are less distinct or a few small pigment dots may be scattered over the entire shell.

Median tooth of radula triangular, with sharply pointed central denticle and 3 or 4 serrations on each border; each of the pair of lateral teeth J-shaped and arranged serially in sequence with lateral teeth. The whole closely resembles the vertebral column and ribs of a vertebrate.

The shell of one male-phase individual and that of another in the transition phase measured 14 by 10 mm, and one in the female phase 18 by 15 mm. These 3 specimens lived inside dead shells of *Astraea undosa* (Wood), while 3 smaller individuals, each about 8 mm long were found on the outside of the shells. Collected at a depth of about 16 meters near North Coronado Island, Lower California (near border of Southern California) by Dr. Carl L. Hubbs and Woodbridge Williams, in December, 1946 and June, 1947. The species is named in honor of Mr. Williams.

Holotype and 1 paratype to be deposited in the museum of the California Academy of Sciences and paratypes in the San Diego Natural History Museum and the U. S. National Museum.

Another Pacific coast species, *C. squama* Broderip, likewise has a flat shell which is also white in color except for a series of narrow, brown, radiating stripes extending nearly half the length of the shell. The type locality is Panama (Smith, '46). In *C. williamsi* the pigmented apical portion is sharply demarcated and occupies only one-sixth to one-fourth the length of the adult shell. The shells of very young individuals both of *C. plana* and *C. nivea* are commonly speckled with reddish-brown dots and although these usually disappear before the shell reaches a length of 3 mm, they may occasionally be retained at the apex of the adult shell or a few small pigment spots may be scattered irregularly or in radiating lines over the entire shell.

The writer is indebted to Dr. G. Dallas Hanna, Dr. L. G. Hertlein and Mr. Allyn G. Smith of the California Academy of Sciences for opinions relative to the identity of the species.

SUMMARY

1. *Crepidula williamsi* is a typical protandric species. The young individual, in the male phase, is motile and provided with a long, protrusible phallus with the sperm groove opening at its end. On the completion of the male phase the phallus is absorbed and all the other male organs become dedifferentiated. The individual thereby returns to a condition of sexual immaturity. Following this transition stage the ovary, oviduct, vagina and sperm receptacles are constructed from the dedifferentiated parts of the former male organs, the individual becomes sedentary for the remainder of life, and female patterns of behavior replace the masculine instincts of early life.

2. These snails are mainly plankton- and detritus-feeders, ingesting, together with much inert material, only minute organisms and organic particles. These are collected from

water passing over the gill, imbedded in mucus and then carried by ciliary action through a long food groove to the mouth. The motile juvenile and male-phase individuals also browse directly on minute animals and algae. For this purpose the radula is essential.

3. This new species differs from others of the genus in having a deeply pigmented shell only in early life. This remains at the apex of the white, porcelaneous shell which covers most of the body of the adult.

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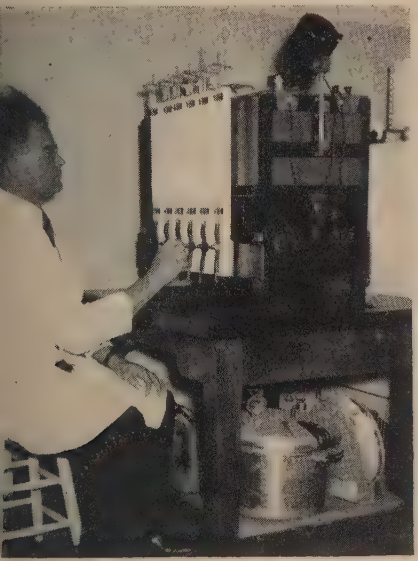
Contribution No. 323

ACTERIAL RELEASE OF OIL OM SEDIMENTARY MATERIALS

by Dr. Claude E. ZoBell*

CERTAIN bacteria promote the removal of oil from oil-bearing formations. This they do by dissolving sedimentary materials, producing gases and detergents or wetting agents, and by bodily crowding oil off from solid surfaces. Some of these bacteriological processes may have contributed to the separation, migration, and accumulation of oil in subterranean deposits during past geological ages. It has been suggested that the introduction of appropriate cultures into certain oil-bearing formations may facilitate the recovery of oil. This paper summarizes some of the preliminary observations on the problem. It is a contribution from the Scripps Institution of Oceanography, New Series No. 000, and likewise a contribution from A.P.I. Research Project 43A at La Jolla, Calif.



The author manipulating the Warburg respirometer which is used to measure the utilization and production of gaseous metabolic products

BACTERIAL dissolution of three different kinds of oil-bearing sedimentary materials has been demonstrated by laboratory experiments. These include the organic remains of plants and animals which contain petroleum hydrocarbons, calcium carbonate, and other calcareous materials, and gypsum or similar sulfate minerals.

Numerous kinds of putrefactive bacteria appear to be responsible for the disintegration of the organic remains of plants and animals. Hydrocarbons produced by plants and animals are often so intimately associated with the tissues of organisms that the hydrocarbons are liberated only after the decomposition of the surrounding organic matrix. The putrefaction of the remains of algae and other organisms is generally accompanied by an increase in the amount of nonsaponifiable oily substance that can be extracted. Part of this increase in oily substance is attributable to the synthesis of hydrocarbons by anaerobic bacteria, but it is believed to be mostly due to the liberation of bound hydrocarbons from the tissues of decomposing organisms.

The liberation of oil bound by organic matrix is a process which is probably of greatest importance in recently deposited sediments, although there are some students of the subject who believe that organically bound hydrocarbons may be preserved in sediments for geologically long periods of time before being liberated by the decomposition of the organic matrix.

Limestone Dissolved by Acids

There are several bacterial processes which help to dissolve limestone, dolomite, or other calcareous materials. A good many kinds of bac-

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*Associate professor of marine microbiology at Scripps Institution of Oceanography of University of California and director of A.P.I. Research Project 43A.

teria produce acids, which promote the dissolution of carbonates. Carbon dioxide produced by respiring bacteria reacts with water to give carbonic acid:

$$CO_2 + H_2O \rightarrow H_2CO_3$$

Carbonic acid, in turn, reacts with calcium carbonate or magnesium carbonate to give the corresponding bicarbonate, which is more soluble in water:

$$H_2CO_3 + CaCO_3 \rightarrow Ca(HCO_3)_2$$

Bacteria ferment various organic compounds, including petroleum hydrocarbons, with the formation of organic acids. Cellulose, for example, is fermented with the formation of butyric, lactic, propionic, acetic, and other carboxylic acids. Fats are fermented with the formation of fatty acids. Higher fatty acids are broken down to lower members of the series which, being more strongly dissociated, are more acidic. Proteins are decomposed with the formation of amino acids. The reductive deamination of amino acids yields more strongly acidic fatty acids.

Acids produced by various bacterial processes dissolve carbonates, thereby releasing adsorbed oil. At the same time void or pore spaces are formed, which provide for the movement or accumulation of oil. Carbon dioxide resulting from the action of acids on carbonates tends to decrease the viscosity of oil, thereby facilitating its flow:

$$CaCO_3 + 2HA \rightarrow CaA_2 + H_2O + CO_2$$

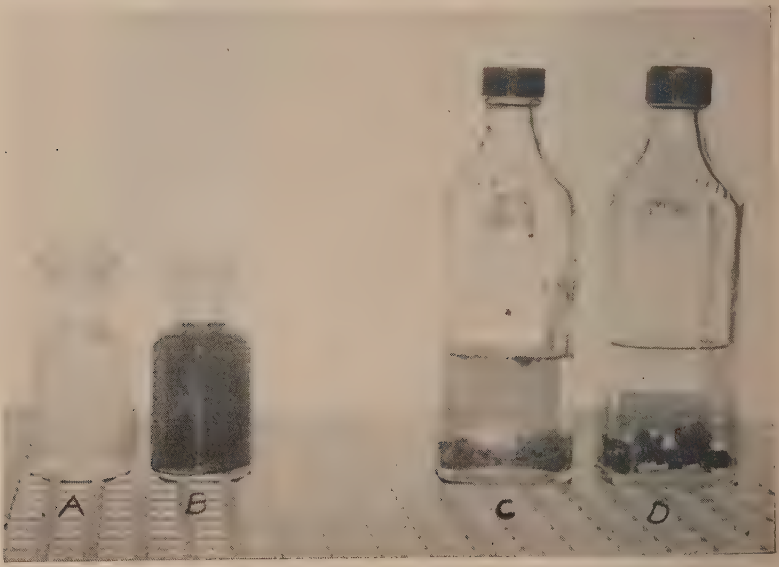
where A is a monovalent acid radical. Carbon dioxide also has a buoyant effect on oil droplets, and if generated in microspheres or structural traps of microscopic dimensions, carbon dioxide may help to expel entrapped oil.

Sulfate Rocks Dissolved

An acid reaction also helps to dissolve gypsum, anhydrite, and similar sulfate minerals, particularly in the presence of active sulfate-reducing bacteria:

$$CaSO_4 + 8H \rightarrow CaS + 4H_2O$$

Sulfate-reducing bacteria can obtain the hydrogen necessary for this reaction from the fermentation of organic matter or from a variety of inorganic reactions. Certain sulfate reducers can utilize petroleum hydro-



Bottles A and B illustrate a method of demonstrating sulfate reduction by bacteria. Both contain nutrient media and soluble iron salts. The iron has been precipitated as black, insoluble ferrous sulfide by the sulfate-reducing bacteria in bottle B. Notice the layer of oil floating on the surface in bottle C, which was released by the action of sulfate-reducing bacteria in nutrient media on Athabaska tar sand. Bottle D contains no bacteria carbons as a source of hydrogen and energy for the reduction of sulfate, and some varieties can utilize molecular hydrogen. Hydrogen may be produced in petroliferous sediments by the action of radioactive substances on hydrogen-containing compounds or it may be produced by chemical reactions in the earth's crust.

At first glance it might appear that the destruction of the strongly acidic sulfate radical (SO_4) would tend to make conditions less acid rather than more acid. It must be taken into consideration, however, that sulfate occurring in the form of poorly soluble gypsum or anhydrite has little effect on the acidity of surrounding fluids. Sulfide ion, which results from the reduction of sulfate, is itself slightly acidic when dissolved in water. Moreover, organic acids formed from carbon compounds, which are oxidized by the sulfate-reducing bacteria as a source of energy, help to make for acidic conditions.

In the laboratory, sulfate reducers have been observed to cause changes in the reaction of unbuffered culture media from an initial value of pH 7.5 or 8.0 to as low as pH 5.8. Such bacteria have been observed to dissolve appreciable quantities of plaster of paris ($CaSO_4 . 2H_2O$), gypsum, and anhydrite and larger quantities of calcium carbonate and magnesium carbonate. In some experiments in which these materials were saturated with oil, their dissolution by sulfate-reducing bacteria resulted in the liberation of oil.

Carbon Dioxide Reduced

Bacteria which reduce carbon dioxide may contribute to the dissolution of carbonates. In the presence of water, carbonates tend to dissociate in the following simplified fashion:

$$CaCO_3 + H_2O \rightarrow Ca(OH)_2 + CO_2$$

The removal of carbon dioxide would cause the reaction to go to the right, particularly if acids produced by other processes neutralized the calcium hydroxide.

The bacterial reduction of carbon dioxide by hydrogen to acetic acid has been reported:

$$2CO_2 + 4H_2 \rightarrow CH_3COOH + 2H_2O$$

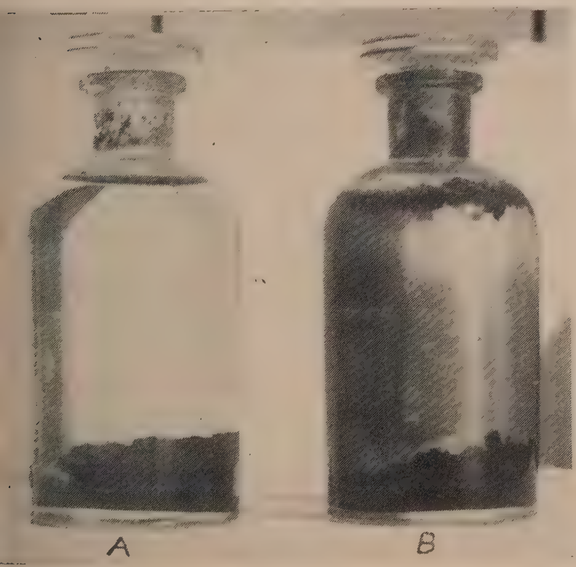
Other carboxylic acids may be formed from the reduction of carbon dioxide by related bacteria. If present in petroliferous sediments, the activity of such acid-producing bacteria could help to account for the porosity of limestone and the accumulation of oil.

Methane Produced by Bacteria

Methane-producing bacteria, which are known to be widely distributed in marine sediments, also reduce carbon dioxide. In fact it is the consensus that all biologically produced methane results from the reduction of carbon dioxide:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$$

Several species of anaerobic bacteria



Bottle B contains Athabaska tar sand and nutrient media in which sulfate-reducing bacteria have grown. Bottle A is a sterile control containing Athabaska tar sand and nutrient media. Note the oil floating on the surface of bottle B which has been released from the tar sand by bacterial action have been shown to be able to convert mixtures of carbon dioxide and molecular hydrogen into methane. Hydrogen for the formation of methane in oil-bearing sediments may come from the fermentation of organic matter, the effect of radioactivity on hydrogen-containing compounds, or from chemical reactions in the earth's crust.

Methane produced in oil-bearing sediments would tend to dissolve oil and to make it more fluid. If produced in micro traps or dead-end cavities containing oil, methane might be instrumental in expelling entrapped oil.

The effects of methane or other products formed by bacteria can be expected to be most pronounced in the localized area in the immediate vicinity of active bacterial cells. This, together with the fact that many varieties of bacteria have an affinity for growing on solid surfaces, fits bacteria rather admirably for removing oil from solids. A minute quantity of methane, for example, produced immediately at the surface of a solid to which oil is attached may have a much greater tendency to release oil than would the presence of appreciably larger quantities of methane a little distance away. Incidentally, most bacteria range in diameter from ½ to 1 micron in diameter, a micron being approximately .0025 in.

Wetting Agents Produced

Detergents or wetting agents produced by bacteria growing on a solid surface coated with oil help to liberate oil. That bacteria produce detergents is indicated by the observation that actively growing cultures reduce the surface tension of the medium by as much as 20 or 20 dynes per centimeter. Culture media having an initial surface tension of 65 to 70 dynes per centimeter have been found to have a surface tension of 50 to 55 dynes following the growth of bacteria. Even when rendered sterile by the addition of phenol, media having reduced surface tensions have been found to liberate oil from oil-saturated sand. The detergents responsible for the reduced surface tension of the medium would probably be even more effective in liberating oil from oil-saturated sand when produced immediately on the surface of the sand particles.

Bacterial Growth on Surfaces

The tendency of some bacteria to grow attached to solid surfaces has been studied by immersing glass slides in liquid cultures for different periods

The E. W. Scripps, the 104-ft. research vessel of the Scripps Institution of Oceanography. This vessel has laboratory space and living accommodations for six scientists and a crew of nine

Main buildings at Scripps Institution of Oceanography, taken from 1,000-ft. pier

of time and then examining the slides microscopically. Such studies have revealed that many bacterial species grow preferentially or exclusively on solid surfaces. Nearly all species have some tendency to attach themselves to solid surfaces. Some attach themselves so tenaciously that they resist removal by rapidly running water or by rubbing with a cotton swab. Further details are to be found in an article by the author entitled, "The Effect of Solid Surfaces Upon Bacterial Activity," published in the Journal of Bacteriology, Vol. 46, pages 39-56, 1943.

It has been observed that certain bacteria have such marked affinity for solids that they attach themselves to and grow on glass slides coated with grease or oil. Bacteria forced themselves under the film of oil or grease and gradually set the latter free to float to the surface of the nutrient medium. After a few days' incubation, microscopic examination of glass slides showed that the entire area was covered by tenaciously attached bacteria and most of the oil was removed. Bacteria which grow on solid surfaces may have a similar effect on particles of sand or other sedimentary material covered with oil.

Can Bacteria Grow in Oil Sands?

Whether any oil-releasing organism could be functional in petroliferous sediments would depend upon the presence of nutrients and favorable environmental conditions. Finding bacteria in recently deposited sediments on the floor of the ocean at the greatest depths examined, and to a lesser extent, in reservoir fluids from oil wells, is highly suggestive that bacteria are alive and active in certain oil-bearing formations. Demonstrating the ability of bacteria to grow in oil-well brines under environmental conditions simulating conditions in subterranean deposits is considered as corroborative evidence.

Most of the bacteria recovered from oil-well brines are either sulfate reducers, methane producers, or hydrocarbon oxidizers, their relative abundance being in the order named. The most physiologically versatile and most widely distributed oil-releasing bacteria have proved to be sulfate reducers. We have isolated from marine sediments varieties of sulfate-reducing bacteria which decompose gypsum, dissolve carbonates, digest organic matter, produce carbon dioxide, form detergents, and attach themselves tenaciously to solid surfaces in appropriate nutrient media. Sulfate-reducing bacteria have been cultivated in samples of certain reservoir fluids or oil-well brines from which atmospheric oxygen has been excluded.

Sulfate Reducing Bacteria

The ability of pure or partially purified cultures of sulfate-reducing bacteria, growing in nutrient media, to liberate oil from samples of Athabaska oil sand, oil-saturated shales, cores of oil-bearing sands, and from synthetic sediments soaked with oil has been demonstrated. However, in none of the experiments has any oil been liberated from samples of oil shale from which no oil could be extracted with ether, acetone, or similar solvents. Likewise bacteria released no oil from samples of natural rock asphalt.

Although the quantity of oil released from oil-bearing sediments has been relatively small, the foregoing observations suggest that bacteria may have played an important role throughout the geological ages in liberation, migration, and accumulation of oil in subterranean deposits. The observations also suggest that the introduction of appropriate bacterial cultures into selected oil-bearing formations may help to increase the recovery of oil.

For this purpose sulfate-reducing bacteria appear to be most promising, by virtue of their physiological versatility and their ability to propagate in reservoir fluids. No one variety of sulfate-reducing bacteria liberates oil from oil-bearing sediments by all of the mechanisms recounted above and no one variety is able to grow under all types of environmental conditions where oil is found, but it may be possible to select cultures which are suitable for each particular set of conditions.

Some sulfate reducers, for example, grow best or only at temperatures ranging from 70°-85° F., others at 85°-100° F., and the range of still others is 140-160° F., etc. Thus if the temperature of the oil-bearing formation ranges from 140°-160° F., it would be necessary to select or develop a strain of bacteria which would grow at this temperature. Some sulfate reducers grow at temperatures as high as 180° F. Others grow at 32° F. or lower. The range between the upper and lower temperature limits at which most cultures will grow is relatively narrow.

Species or strains of sulfate reducers differ greatly in their salinity tolerance. *Desulfovibrio desulfuricans*, for example, grows in fresh-water media but not in sea-water media (salinity about 35,000 p.p.m.). *Desulfovibrio aestuarii* grows in sea water or isotonic salt solutions but not in fresh-water media. *Desulfovibrio halohydrocarbonoclasticus* requires a salinity of 100,000 to 300,000 p.p.m.

It may be of interest to point out that the imposing technical names of the bacteria are made up of simple descriptive Greek roots: *Desulfo* means sulfate reducing and *vibrio* means a comma or spiral-shaped organism. In the species name, *halo* means salt, since this variety requires much salt for its growth. The suffix *clasticus* means splitting or breaking apart, which, when appended to *hydrocarbon*, denotes that hydrocarbons are attacked. It is much easier and more explicit to say or write *Desulfovibrio halohydrocarbonoclasticus* than it is to say "a comma-shaped bacterium which attacks hydrocarbons in a medium containing considerable salt." Its cousins which do not require high concentrations of salt are designated *D. hydrocarbono-*

The personnel of A.P.I. Research Project 43A: Dr. W. D. Rosenfeld, D. M. Updegraff, Helen H. Whelply, F. D. Sisler, Dr. C. E. ZoBell, and W. E. Hutton *clasticus*, or simply *D. HC* in the laboratory.

Different cultures of sulfate-reducing bacteria also have different pH and carbon or energy requirements. The last named species, for example, can utilize higher paraffinic hydrocarbons as a source of energy, and some strains can utilize molecular hydrogen. Other strains require lactates or similar compounds for their growth and multiplication. Their nitrogen requirements are satisfied by ammonium.

Movement in Sediments

In order to be effective in releasing oil, bacteria must be able to propagate in reservoir fluids and to permeate oil-bearing formations. Being actively motile, sulfate-reducing bacteria are not dependent upon the movement of reservoir fluids for their dissemination. Not only do sulfate reducers swim about actively but they propel themselves along surfaces and through capillary spaces by a process known as protoplasmic extrusion or extension.

In long glass tubes packed with mixtures of sand, calcium carbonate, and calcium sulfate soaked with nutrient medium, sulfate-reducing bacteria have been observed to migrate at an average rate exceeding 1 in. per day. The rate of migration was equally rapid in all directions; upward, downward, and horizontally. These and similar observations indicate that, if successfully implanted in an oil-bearing formation, sulfate-reducing bacteria might be expected to permeate the formation in all directions.

Words of Warning

The observations summarized above are based upon laboratory observations. Operators who are interested in applying the bacterial process to the secondary recovery of oil are warned that it is a tremendously large step from the test tube to an oil well. Whether sulfate reducers, methane producers, hydrogen producers, or other types of bacteria in pure culture or combinations will grow and liberate oil from oil-bearing sediments in subterranean deposits as they do in test tubes is purely conjectural. Before any positive recommendations can be made, much more experimental and development work will have to be done by trained microbiologists working in close cooperation with petroleum engineers. Although it is definitely a wildcat proposition with the odds against immediate success, the vast quantities of oil locked in sediments should offer adequate incentive for a thorough exploration of the possibilities of the bacteriological process.

Successful implantation of oil-releasing bacteria into oil-bearing materials will require considerable knowledge of the bacteria and the formation. One must be guided in the selection of appropriate bacterial cultures by the temperature, salinity, pH, utilizable organic content, and other environmental conditions that might influence bacterial multiplication and activity. Samples should be examined to ascertain if bacteria are already present in the formation. Finally preliminary tests should be made in the laboratory to demonstrate the ability of oil-releasing bacteria to grow in the reservoir fluids.

Injurious bacteria must be avoided; some bacteria modify or actually destroy crude oil. (See article by author entitled, "Action of Microorganisms on Hydrocarbons," appearing in Bacteriological Reviews, Vol. 10, pp. 1-49, 1946). Some bacteria have a corrosive effect on iron or steel structures. The growth of other injurious types of bacteria clog oil sands rather than increasing the porosity or permeability. It should be comforting to know that the most effective oil-releasing bacteria are harmless to man and have no deleterious effect on oil.

Summary and Conclusions

There are several mechanisms by which bacteria can liberate oil from oil-bearing sediments. Test-tube experiments indicate that the dissolution of limestone or other calcareous materials is one of the most important mechanisms. Sulfate minerals are also decomposed by sulfate-reducing and acid-producing bacteria. The selective action of bacteria on the remains of organisms may liberate bound hydrocarbons.

Carbon dioxide, methane, or hydrogen produced by bacteria in microtraps may promote the flow of oil. Wetting agents or detergents formed by bacteria help to remove oil from sediments, particularly when the bacteria grow on the surface of solids. The growth of bacteria on solid surfaces tends to crowd off oil films.

Laboratory experiments have demonstrated the bacterial release of oil from samples of Athabaska oil sands, various kinds of oily shales, a large variety of synthetic sediments saturated with oil, and from a few diamond-drilled cores of oil-bearing sands. Negative results only were obtained with samples of oil shale and natural rock asphalt.

Sulfate-reducing bacteria appear to be the most versatile oil-releasing organisms. Recent experiments, however, indicate that methane-producing, hydrogen-producing, and other anaerobic bacteria growing either in pure culture or in combinations may be more effective if it proves to be practicable to inject them in oil-bearing formations with appropriate nutrients.

No specific recommendations can be made at this time except that much more research work is indicated by the possibilities. Properly planned investigations by trained microbiologists working in cooperation with petroleum geologists, chemists, and engineers can be expected to produce practical results applicable to the problem of petroleum recovery.

Acknowledgments

It is a pleasure to acknowledge the technical assistance and suggestions of W. E. Hutton, W. D. Rosenfeld, F. D. Sisler, D. M. Updegraff, Helen H. Whelply, and Jean S. ZoBell. Members of the A.P.I. Advisory and Receiving Committees have also made important contributions.

Carl A. Young was instrumental in securing U. S. Patent No. 2,413,278 covering the bacteriological process for recovering oil, which has been dedicated to the public without charge in compliance with the policy of the American Petroleum Institute and University of California. The Pennsylvania Grade Crude Oil Association also made important contributions to the study of the problem which helped to secure patent protection for the public. The support and cooperation of members of its research committee, including Dr. Richard V. Hughes, director of production research, is also acknowledged.

The author appreciates the interest exhibited in these investigations by oil producers, hundreds of whom have requested additional information and some of whom have offered the use of oil wells for field experiments. Unfortunately, however, we have neither the time, facilities, nor funds to acknowledge these requests and offers except through technical or trade journals such as The Oil and Gas Journal, which can be depended upon to keep you informed regarding significant developments.

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Contribution No. 324

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WIND-DRIVEN CURRENTS IN A BAROCLINIC OCEAN; WITH APPLICATION TO THE EQUATORIAL CURRENTS OF THE EASTERN PACIFIC*

BY H. U. SVERDRUP

SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA, LA JOLLA, CALIFORNIA

Communicated July 31, 1947

1. *Introduction.*—Permanent ocean currents are computed from the observed distribution of density on the assumptions (1) that the horizontal pressure gradient is balanced by the Coriolis force (the deflecting force of the earth's rotation) and (2) that the horizontal velocities and the hori-

zontal pressure gradient vanish at a moderate depth below the sea surface. The second condition can be fulfilled only in a baroclinic system, that is, in a system in which the isosteric surfaces intersect the isobaric surfaces.

In the computation of currents acceleration and frictional forces are neglected. Experience indicates that the computations lead to nearly correct results, implying that accelerations and frictional forces are small, but since friction is not entirely lacking, energy must be supplied to the ocean in order to maintain the permanent currents and the corresponding permanent distribution of mass. This energy can be supplied by the effects of heating and cooling or by the stress which the prevailing winds exert on the sea surface. Of the sources the latter is generally considered to be the more important. We shall examine effects of the wind stress only, taking into account that the ocean waters in motion represent a baroclinic system.

Ekman[1] and Stockmann[2] have examined the currents which develop in a *homogeneous* ocean under the influence of a stress exerted on the free surface, and Fjeldstad[3] has solved a special problem dealing with baroclinic conditions. If the general problem for a baroclinic ocean could be solved, knowledge of the wind stress alone would enable us to compute the permanent ocean currents, provided the effects of heating and cooling were negligible. A treatment of this general problem would present great mathematical difficulties because it would require the introduction of lateral frictional stresses and complete boundary conditions. Here we shall deal with the special case of equatorial currents in a region where lateral stresses can be neglected, boundary conditions are relatively simple, wind systems are semipermanent, and where our results imply that effects of heating and cooling, if present, need not be considered explicitly.

The striking feature of the currents of the equatorial regions is that imbedded between the currents which flow toward the *west* under the influence of the prevailing trade winds equatorial counter currents flow toward the *east*. In the Pacific and Atlantic Oceans the counter current is particularly well developed in the eastern parts of the oceans where it is located north of the equator, its axis coinciding approximately with the location of the equatorial calm belt which is found further to the north in summer than in winter. In the Indian Ocean the counter current is found to the south of the equator, but in the northern winter only.

Our specific problem is to determine whether the equatorial currents, including the counter currents, can be accounted for on the basis of our knowledge of the wind stress only. This problem was first approached by Montgomery and Palmén,[4] but Stockmann[2] has shown that they did not treat it in a sufficiently general manner. Stockmann's theoretical results, however, are not applicable to the conditions in the ocean because he assumed homogeneous water, but a similar analysis for a baroclinic system leads to a remarkable agreement between theoretical conclusions and observed conditions.

2. *Theory.*—The ocean waters are so nearly in hydrostatic equilibrium that at any depth the pressure, p, can be determined by a numerical integration of the hydrostatic equation:

$$dp = g\rho\, dz \tag{1}$$

provided that the density, ρ, is known from observations. In equation (1) and in the following equations the z-axis is positive downwards.

Neglecting lateral stresses the equations of horizontal motion can be written:

$$\begin{aligned} \frac{\partial u}{\partial t} + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} &= -\frac{1}{\rho}\frac{\partial p}{\partial x} + \lambda v + \frac{1}{\rho}\frac{\partial}{\partial z}\left(A\frac{\partial u}{\partial z}\right) \\ \frac{\partial v}{\partial t} + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} &= -\frac{1}{\rho}\frac{\partial p}{\partial y} - \lambda u + \frac{1}{\rho}\frac{\partial}{\partial z}\left(A\frac{\partial v}{\partial z}\right) \end{aligned} \tag{2}$$

where u and v are the horizontal velocity components in a rectilinear coordinate system, $\lambda = 2\omega \sin \varphi$ (ω the earth's angular velocity of rotation, φ the latitude, taken positive to the north of the equator), and A is the eddy viscosity.

We shall assume stationary conditions,

$$\frac{\partial u}{\partial t} = \frac{\partial v}{\partial t} = 0, \tag{3}$$

and shall neglect the non-linear terms, the field accelerations:

$$u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} = u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} = 0, \tag{4}$$

thereby placing severe restrictions upon the possible lateral boundary conditions. Equations (2) reduce to:

$$\begin{aligned} \frac{\partial p}{\partial x} &= \lambda\rho v + \frac{\partial}{\partial z}\left(A\frac{\partial u}{\partial z}\right) \\ \frac{\partial p}{\partial y} &= -\lambda\rho u + \frac{\partial}{\partial z}\left(A\frac{\partial v}{\partial z}\right) \end{aligned} \tag{5}$$

stating that the horizontal pressure gradient is balanced by the Coriolis force and frictional stresses exerted on horizontal surfaces. In *homogeneous* water the horizontal pressure gradient is independent of depth but in a *baroclinic* system varies with depth. In the ocean it generally vanishes at a moderate depth, less than that to the bottom. We define a function P by the integrals

$$\frac{\partial P}{\partial x} = \int_0^d \frac{\partial p}{\partial x} dz, \qquad \frac{\partial P}{\partial y} = \int_0^d \frac{\partial p}{\partial y} dz \tag{6}$$

where d is equal to or greater than the depth at which the horizontal pressure gradient becomes zero. The function P, which is closely related to the P-function introduced by Ekman,[5] can be computed from the observed vertical distribution of density at a single oceanographic station, using equation (1).

The horizontal velocity must vanish at or above the depth d. The integrals

$$M_x = \int_0^d \rho\, u dz, \qquad M_y = \int_0^d \rho\, v dz \tag{7}$$

represent therefore the components of the *net* mass transport by the currents.

Integrating equations (5) from 0 to d, and introducing the horizontal boundary conditions:

$$\begin{aligned} \left(A\frac{\partial u}{\partial z}\right)_0 &= -\tau_x, & \left(A\frac{\partial u}{\partial z}\right)_d &= 0 \\ \left(A\frac{\partial v}{\partial z}\right)_0 &= -\tau_y, & \left(A\frac{\partial v}{\partial z}\right)_d &= 0 \end{aligned} \tag{8}$$

where τ_x and τ_y are the components of the wind stress, we obtain:

$$\frac{\partial P}{\partial x} = \lambda M_y + \tau_x \tag{9a}$$

$$\frac{\partial P}{\partial y} = -\lambda M_x + \tau_y \tag{9b}$$

The terms in equations (9) are well known in oceanography. Omitting the stress components the equations give the mass transport related to the distribution of density, or assuming homogeneous water in hydrostatic equilibrium ($\partial P/\partial x = \partial P/\partial y = 0$) they give the mass transport by pure wind currents. Equations (9) have been used by Defant[6] for computing the wind stress from oceanographic observations, including direct measurements of currents, but they have not been applied to other problems.

For application to other problems we add the equation:

$$\frac{\partial M_x}{\partial x} + \frac{\partial M_y}{\partial y} = 0 \tag{10}$$

which is obtained by integration of the equation of continuity, assuming hat the vertical velocity is zero at the free surface and at the depth d. The three equations (9a), (9b) and (10) can be considered as relating the hree unknown quantities, P, M_x, and M_y, to the known wind stress. Conequently, the distribution of density, as described by the partial derivaives of P, and the mass transport by the corresponding currents can be xpressed as functions of the stress.

In applying equations (9) and (10) to equatorial currents we place the ositive x-axis toward the east and the positive y-axis toward the north, nd let $y = 0$ at the equator ($\varphi = 0$). Since

$$dy = R\,d\varphi \tag{11}$$

here R is the radius of the earth:

$$\frac{\partial\lambda}{\partial x} = 0, \qquad \frac{\partial\lambda}{\partial y} = \frac{2\omega\cos\varphi}{R}, \qquad \frac{\partial^2\lambda}{\partial y^2} = -\frac{2\omega\sin\varphi}{R^2} \tag{12}$$

Differentiating equation (9a) with respect to y and (9b) with respect to , subtracting and taking equations (10) and (12) into account, we obtain

$$M_y\frac{\partial\lambda}{\partial y} + \left(\frac{\partial\tau_x}{\partial y} - \frac{\partial\tau_y}{\partial x}\right) = 0 \tag{13}$$

n the trade-wind belt of the eastern Pacific the term $\partial\tau_y/\partial x$ is so small at with good approximation:

$$M_y = \frac{\partial\tau_x}{\partial y}\Big/\frac{\partial\lambda}{\partial y} = -\frac{\partial\tau_x}{\partial y}\,\frac{R}{2\omega\cos\varphi} \tag{14}$$

troducing equation (14) in (9a):

$$\frac{\partial P}{\partial x} = -\frac{\partial\tau_x}{\partial y}R\tan\varphi + \tau_x \tag{15}$$

, writing differences on the left-hand side:

$$\frac{\Delta P}{\Delta x} = -\overline{\frac{\partial\tau_x}{\partial y}}R\tan\varphi + \bar{\tau}_x \tag{16}$$

here averages over the distance Δx are indicated by bars.

From equations (10) and (14) follows

$$\frac{\partial M_x}{\partial x} = \frac{1}{2\omega\cos\varphi}\left(\frac{\partial\tau_x}{\partial y}\tan\varphi + \frac{\partial^2\tau_x}{\partial y^2}R\right) \tag{17}$$

hen integrating equation (17) from 0 to Δx we shall assume a north-south rtical boundary at $x = 0$ at which the kinematic boundary condition $= 0$ must be satisfied in the form $M_6 = 0$. We obtain:

$$M_x = \frac{\Delta x}{2\omega \cos \varphi}\left(\frac{\overline{\partial \tau_x}}{\partial y} \tan \varphi + \frac{\overline{\partial^2 \tau_x}}{\partial y^2} R\right) \qquad (18)$$

Equation (18) cannot hold at a second north-south boundary at, say, $x = L$, at which the condition $M_L = 0$ must be satisfied. This inadequacy of our solution is due to the neglect of the field accelerations (eq. 4). Attempts will be made to find more general solutions and to study other special cases.

Substituting equation (18) in (9*b*):

$$\frac{\partial P}{\partial y} = -\Delta x \tan \varphi . \left(\frac{\overline{\partial \tau_x}}{\partial y} \tan \varphi + \frac{\overline{\partial^2 \tau_x}}{\partial y^2} R\right) + \tau_y \qquad (19)$$

Equations (15) or (16) and (19), together with (14) and (18), represent in our special case the relationships of the distribution of mass and the corresponding mass transport to the wind stress. The validity of our results can be tested where suitable observations are available.

3. *Discussion*.—The available oceanographic observations comprise (1) a line of 8 stations between latitudes 22°N and 10°S, longitudes 137°W and 162°W, occupied by the *Carnegie* between October 21 and November 4, 1929 (Fleming[7]); (2) a line of 12 stations between latitudes 6°N and 9°S, longitudes 80°W and 108°W, occupied by the *Carnegie* between October 26 and November 21, 1928; and (3) a line of 8 stations between latitudes 9°N and 21°N, longitudes 87°W and 109°W, occupied by the Bushnell between March 18 and March 24, 1939 (Sverdrup[8]). From the observations at each of these stations the value of the function P was computed by integrating to a depth of 1000 meters. From all data the ratio $\Delta P/\Delta x$ was found, and from the *Carnegie* section in mid-ocean $\partial P/\partial y$ was derived.

Wind observations comprise (1) monthly wind roses for 5-degree squares published in the Pilot Charts of the North and South Pacific, giving the percentage of winds from different directions and the corresponding average wind force (on the Beaufort scale) and (2) compilations of frequencies of winds of different forces in the "Atlas of Climatological Charts of the Oceans."[9] From the wind data the average wind stresses in October and November were computed, using the relationship

$$\tau = \gamma^2 \rho' U^2$$

where γ^2 is the resistance coefficient, ρ' the density of the air, and U the wind speed as estimated at a height of about 10 meters. At wind force 3 Beaufort or less the sea surface was assumed to be hydrodynamically smooth, with a resistance coefficient of about 0.8×10^{-3}, decreasing somewhat with increasing wind speed. At wind force 4 Beaufort and higher a constant value, $\gamma^2 = 2.6 \times 10^{-3}$, was used, corresponding to a hydrodynamically rough surface (Rossby[10]). The manner in which all computations were carried out will be described elsewhere by the author and R. O. Reid, who has prepared the figures in this paper.

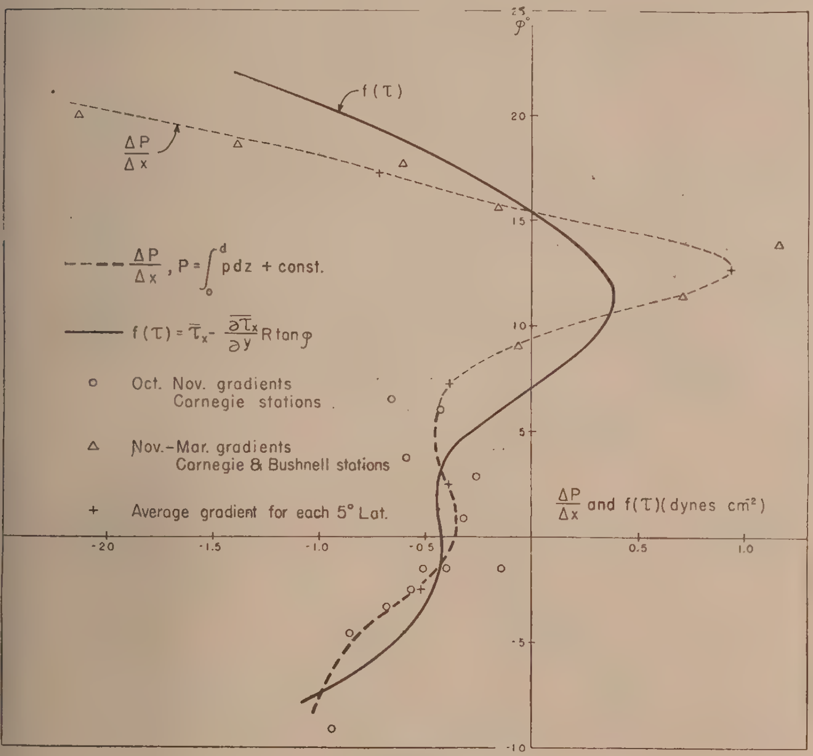

FIGURE 1

In figure 1 the terms of equation (16) are shown as functions of latitude. The curve that represents the left-hand term is heavily dashed to the south of latitude 6°N where the oceanographic observations upon which it is based were all taken in October–November, although in different years. To the north of 6°N the curve is shown by light dashes because observations off the American west coast in March have been combined with observations in mid-ocean in October. The right-hand term, the stress function, is shown by a full-drawn curve and is based on climatological wind data for the months October–November. The agreement between the curves is very good, considering that results of average wind conditions are compared with results derived from a few oceanographic stations which have been occupied in different seasons.

In figure 2 the P function and the terms of equation (19) are plotted against latitude. The P function is based on the *Carnegie* observations in mid-ocean in October–November, 1928, and the stress function on the average wind conditions in October–November over the ocean from the American west coast to the *Carnegie* section. A good agreement is obtained between the results based on a single oceanographic section and those derived from climatological wind charts.

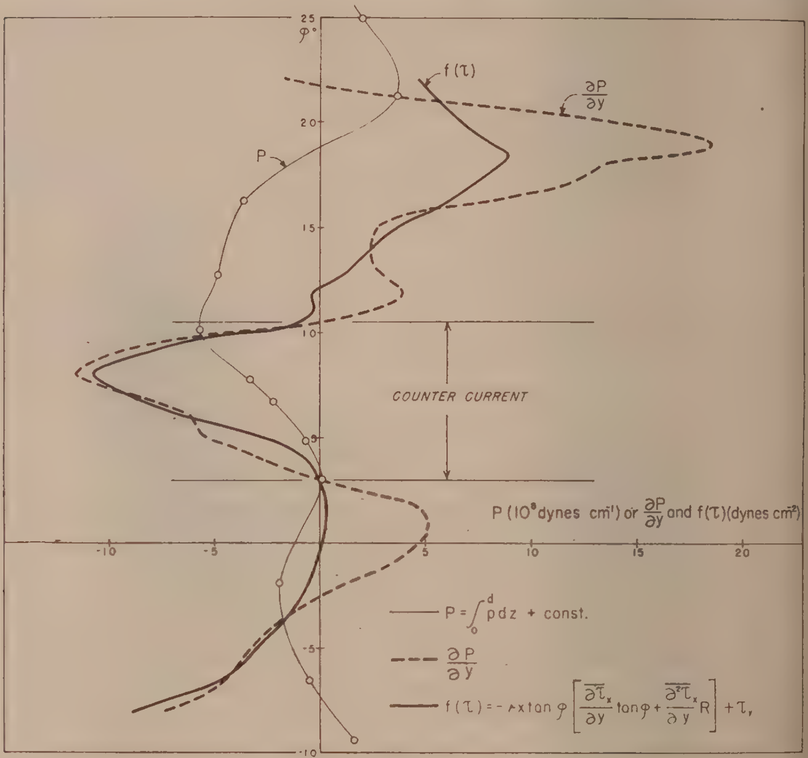

FIGURE 2

4. Conclusions.—The distribution of density and the mass transport by the accompanying currents of the eastern equatorial Pacific depend entirely upon the average stress exerted on the sea surface by the prevailing winds. This conclusion is probably valid for the equatorial currents of all oceans but it has been demonstrated only for a case in which the non-linear terms in the equation of motion can be neglected.

It appears possible that the analysis of the relationship between wind stress and prevailing currents, assuming baroclinic conditions, can be extended to other cases and can be developed into a powerful tool for examining permanent currents as well as changes produced by changing winds. Efforts in this direction are being continued.

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CAROTENOID AND INDOLIC BIOCHROMES OF ANIMALS[1]

By Denis L. Fox
Scripps Institution of Oceanography, University of California,
La Jolla, California

Among the more tangible and revealing aspects of comparative animal biochemistry are problems surrounding the various biochromes or natural pigments (45). The number of known naturally occurring colored molecules is steadily increasing, while nutritional, genetic, clinical, and pathological studies are gradually yielding important information regarding some of the physiological features of several pigment classes. But a full understanding of the biochemical significance and metabolic economy of animal biochromes is to be gained only by comprehensive researches along a highway which, although broad, is likewise long and difficult. The great pigmentary variations among animals according to species, sex, particular tissues, season, physiological condition, nutrition, hereditary background, and other factors are sufficient to suggest the scope of the field.

Because of the necessary limitation of space, and in view of the existing wealth of information concerning the carotenoids and indoles (including indigoids and melanins) this review will be devoted to certain comparative aspects of these two outstanding biochrome classes.

In the interests of breadth which must be a part of any comparative survey of this kind, references to certain of the older researches and surveys are desirable and indeed unavoidable.

CAROTENOIDS

The carotenoids of animals commonly occur dissolved in minute oil droplets, to which they impart yellow, orange or red colors; alternately, such compounds may be conjugated with proteins to give blue, green, violet, pink, brown, gray, or other hues.

Carotenoids of several classes are stored in numerous tissues and at various concentrations by animals in the evolutionary scale from Protozoa to the highest vertebrates, including man. As is true among bacteria and fungi, however, there are notable exceptions throughout the animal phyla. Some invertebrates and numerous mammalian species deposit no significant traces of colored carotenoids in their tissues. The great majority of animals, however, store such pigments in their adipose tissue, eyes (e.g., as visual purple) or other photoreceptors, reproductive and other glandular organs, and in integumentary cells or products, e.g., birds' feathers.

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 325.

The chemistry and nomenclature of the carotenoids are discussed amply in various works (10, 65, 118, 123, 186, 193); we shall here consider some aspects of the occurrence and disposition of carotenoids in various animal phyla.

PROTOZOA

In this phylum we are bound to consider not only the true animal organisms but the flagellated phytozoans (e.g., *Euglena*, etc.) as well. Certain green euglenoid flagellates, pursuing a holophytic existence, lose their chlorophyll when deprived of light, becoming saprophytic or even holozoic, but retaining the red pigment of the "eye-spot."

Carotenoids in certain species of phytozoa give rise to the conspicuous yellow, orange, or red colors sometimes observed in snow, rain ponds, lakes, salt ponds, and patches in the sea (9, 50, 57, 106, 147). Parasitic infusorians have been observed to acquire carotenoid pigmentation by consuming the eyes of certain crustaceans (20).

SPONGES

Numerous poriferan species show brilliant orange, yellow, red, or purple pigments, whose lipophilic character was recognized by Krukenberg (82) more than sixty years ago. Qualitative chemical examination of extracts of a number of sponge species by Lönnberg (97, 98, 99) and Lönnberg and Hellström (103) revealed the carotenoid nature of the pigments.

From the red sponge *Axinella crista-galli* Karrer and Solmssen (79) have crystallized astacin, the red acidic tetraketo carotenoid derivative of astaxanthin (86) common in many crustaceans. Another red sponge, *Suberites domuncula*, was reported by Karrer & Solmssen (79) to yield a similar red carotenoid with a single absorption maximum at 500 mμ in carbon disulfide. However, Lederer (92) failed to detect such a compound in the same species; he encountered neither acidogenic carotenoids nor xanthophylls, but reported substantial amounts of two suspected hydrocarbons resembling torulene (characteristic of red torulas) and lycopene (of tomatoes) respectively. *Ficulina ficus* likewise yielded isomers or derivatives of lycopene, as well as α- and β-carotenes, found also in *Suberites*.

Drumm & O'Connor (26) and Drumm *et al.* (27) found no astaxanthin in the red sponge *Hymeniacidon sanguinea*, but crystallized from this species both echinenone, the ketonic provitamin A from echinoids (94) and γ-carotene. Drumm and his colleagues suggest that the common presence of echinenone in both sponges and echinoids may indicate a phylogenetic relationship between these two animal groups.

From a comparative biochemical standpoint, the apparent preponderance of carotenes over xanthophylls in some sponges is quite striking, since marine algae, fishes, and the great majority of invertebrates investigated store chiefly xanthophyllic carotenoids in their tissues (52).

COELENTERATES

In this phylum, which includes the jellyfishes, sea anemones, corals, and their allies, we encounter the greatest variety and brilliance of animal pigmentation. The latest reviews on the subject have been written by Lederer (93) and by Fox & Pantin (49).

The fleshy parts of anemones and corals owe their various red, orange or yellow colors to carotenoids, while even some of the blue jellyfish, e.g., the siphonophore *Velella spirans*, acquire their striking color through the conjugation of carotenoids with protein (70, 81). The numerous papers of Lönnberg (97, 98, 99, 102) provide an extended list of coelenterates in which carotenoids were qualitatively demonstrated.

It has been established by M. & R. Abeloos-Parize (3) that the red, brown, and green varieties of *Actinia equina* derive their carotenoids originally from the diet, and that the color variants exhibit a striking specificity either in the primary selective assimilation of a particular carotenoid or in the metabolism of a common compound assimilated by both variants. A new, unstable acidogenic carotenoid, actinioerythrin, occurs in the red variety of *Actinia* *equina*, while the green form possesses also a red-orange xanthophyll which, when conjugated with protein, provides the green color. Both red and green forms yield α- and β-carotenes (40, 71, 88). Newly described xanthophylls, sometimes accompanied by smaller quantities of familiar carotenes, are reported to occur in *Anemonia sulcata*, *Metridium senile* (=*Actinoloba dianthus*) and *Tealia felina* (71).

An acidogenic carotenoid, closely resembling one reported by Heilbron *et al.* (71) to occur in *Tealia felina*, was discovered by Fox & Moe (47) in the small Pacific Coast anemone *Epiactis prolifera*. Fox & Pantin (48) encountered considerable assortments of carotenoids, in widely varying quantities, in the numerous color-phases of the plumose anemone *Metridium senile*. In general, red forms contain the greatest quantities (e.g., nearly 15 mg. per cent), but fewer different carotenoid compounds, while the melanistic brown varieties yield the lowest quantities, but in the greatest and most variable assortments.

While *Metridium senile* stores the carotenoid material in its own tissues, *Cribrina xanthogrammica* has been shown by Strain *et al.* (154) to owe its kinds and quantities of such pigments to the presence of symbiotic algae (zooxanthellae) living within the host.

WORMS

While the platyhelminth, nemertean, annelid, and gephyrean worms provide representatives which are richly colored, relatively little study has been devoted to the carotenoids in these phyla. Actually, hemes and melanins are encountered more frequently in the annelids and sipunculids, while the nemertean forms often exhibit integumentary carotenoids (97, 98, 99, 102, 103, 107).

Sumner & Fox (162) found about 0.36 mg. of carotene per hundred grams of fresh tissues of the blood-red hemoglobin-containing polychaete *Thoracophelia mucronata*. The carotene seemed to be a mixture of the α- and β- isomers, while no xanthophylls or acidogenic carotenoids were encountered.

ECHINODERMS

Bright carotenoid colors abound in the tissues of this group, expecially in the integument, digestive glands, and eggs of sea-stars and in the epidermis of numerous brittle stars. It is worthy of note that such carnivorous classes as these contain the highest concentrations of carotenoids, in contrast to the herbivorous or omnivorous echinoids and holothurians. Furthermore, oxygenated carotene derivatives, including acidogenic compounds and neutral xanthophylls or their esters predominate greatly over carotenes in the asteroid class, while certain ophiuroids store no carotenes at all. On the other hand, several species of echinoids store no acidogenic carotenoids, and yield more carotenes than xanthophylls. One species of holothurian, *Stichopus californicus*, contains very low and approximately equal quantities of carotenes and xanthophylls. The ketonic carotenoid echinenone has been observed in several species of echinoids examined, and in small quantities in the holothurian *Stichopus* but has not been detected in the asteroids save possibly in *Astropecten californicus* (51).

The sea-stars frequently manifest rich blue, purple, violet, pink, or brown colors which arise from the presence of acidogenic carotenoids conjugated with protein (51). Euler & Hellström (36) isolated one such deep blue chromoprotein from the skin of the star *Asterias rubens*. Euler, Hellström & Klussmann (37) suggested that this carotenoid-protein complex might serve the animal as a photoreceptor. Euler & Hellström (36) have separated similar carotenoids, usually bound as chromoproteins, from the integument of other stars, e.g., *Crossaster papposa*, *Solaster endica* and *Porania pulvillus*, while Karrer & Solmssen (79) and Karrer & Benz (78) recovered astacin from *Echinaster sepositus* and *Ophidiaster ophidianus*.

Species of ophiuroids (brittle stars) examined by Fox & Scheer (51) yielded relatively high concentrations of free and esterified xanthophylls and acidogenic carotenoids. Many of the pigment fractions were unique, but so chemically unstable in air as to preclude a thorough investigation.

The echinoids store major quantities of carotenoids in their gonadal and intestinal tissues. Lederer (90, 92) found α- and β-carotenes, accompanied by echinenone, pentaxanthin and other xanthophylls, in the gonads of *Strongylocentrotus lividus*. Fox & Scheer (51) encountered large stores of carotenoids in the intestine and gonads of both male and female *Strongylocentrotus purpuratus* and *Lytechinus pictus*. In the former species the ovarian carotenoids exceeded by threefold the quantities found in the spermaries (i.e., 2.00 vs. 0.69 mg. per cent respectively); in both sexes the gonad pigments were found to be entirely carotenes. In *Lytechinus pictus*, which contains similar concentrations of carotenoids, the spermaries yielded some fourfold as much carotene and about twice as much xanthophyll as were found in ovaries. Carotenes predominate over xanthophylls in the gonads and in most other tissues of *Lytechinus*. In contrast to the asteroids and ophiuroids, the echinoids examined possess but traces of carotenoid in the integument, but carry there instead large quantities of the quinone pigment echinochrome.

MOLLUSKS

Lönnberg (97, 98, 99, 102) has demonstrated carotenoids in nearly eighty molluscan species, including many pelecypods and gastropods and a few amphineuran and cephalopod forms. Ripe eggs, digestive gland and, in some species, skin and eyes yield substantial amounts of the pigments. Lederer (88, 92) and Fabre & Lederer (40) recovered a nonacidic xanthophyll, glycymerin, from the ripe gonads of the scallop *Pectunculus glycymeris*. This unique carotenoid is reported not to be invariably present in the scallop, however (92). From the red gonads and mantle of another scallop, *Pecten maximus*, was recovered an additional new xanthophyll, pectenoxanthin, accompanied by small amounts of esterified xanthophylls and β-carotene. High seasonal variations are reported in the carotenoid content of this mollusk (92). A nonacidic xanthophyll, similar to pectenoxanthin and partly conjugated with protein, was isolated from the gonads of the mussel *Volsella modiolus* by Euler *et al.* (37). Red tissues of other mollusks such as the cockle *Cardium tuberculatum* and the scallop *Pecten jacobaeus* yield various xanthophylls, while an astacin-like compound has been reported in the gastropod *Pleurobranchus elegans* (79). Astacin has been crystallized from red tissues of the scallop-like bivalve *Lima excavata* (150).

Gonads, digestive diverticulum and integumentary tissues of the California mussel *Mytilus californianus* have been found by Scheer (142) to yield a considerable variety of xanthophylls and a new acidic carotenoid mytiloxanthin, but no carotenes. Females possess higher concentrations of total pigments than do males (i.e., average values of nearly 5 mg. as compared with about 2 mg. per cent in fresh tissues). The carotenoids attain their highest concentrations in the gonads, but female somatic tissues also exceed corresponding male tissues in quantities of carotenoids. Oysters have been reported to contain relatively rich stores of vitamin A (75).

The cephalopods seem to be generally poor in carotenoids, although the two-spotted octupus *Octopus bimaculatus* carries appreciable quantities, e.g., up to 8 mg. per cent of wet tissue, in the "liver," and actually secretes xanthophylls and acidogenic carotenoids in the black ink, in quantities up to 0.7 mg. per cent. Other tissues of this species contain no carotenoids, or only traces, the eyes containing a little (46).

Lönnberg (101) found carotenoids in the eyes of *Sepiola scandica*, *Rossia macrosoma* and *Eledone cirrosa*. None of the three species yielded integumentary carotenoids, but *Eledone* liver contained appreciable quantities.

Wald (180) found vitamin A and retinene in the retina of the squid *Loligo pealii*, but no traces of carotenoids in the other tissues. Similarly, Fox & Crane (46) recovered traces of carotenoids from the eyes and accessory nidimental glands of *Loligo opalescens*, but none, or only questionable traces, in other tissues. Of the carotenoids in the liver of *Octopus bimaculatus*, lutein, or a xanthophyll closely resembling it, is a prominent representative, accompanied by smaller amounts of less familiar xanthophylls, β-carotene and an unfamiliar carotene, and a unique carotenoid acid which appears following treatment with alkali. The same compounds, with the exception of carotenes but including xanthophyll esters, are secreted into the ink. Starvation brings about a disappearance of carotenoids from liver and ink. However autolysis of whole or minced liver results in but very slow loss of the pigments.

ARTHROPODS

Crustaceans.—Because of their brilliant colors, vast numbers of species and ubiquitous distribution, the arthropods have been extensively studied. Early investigations were conducted by Verne (172 to 175) on the red carotenoid material in the hypodermal chromatophores, blood, carapace, eyes, and eggs of numerous decapod crustaceans such as *Homarus*, *Astacus*, *Palinurus* and *Cancer*. Similar pigments were encountered as blue or other colored protein complexes in species of *Homarus*, *Astacus*, *Galathea*, *Porcellana*, *Hippolyte*, *Athanas*, *Palaemon*, *Portunus*, *Palinurus*, *Nephrops*, *Dromia*, *Carcinus* and *Pagurus*.

Basing his conclusions upon studies of carotenoids in eggs, eyes and other tissues of the copepod *Idya furcata*, Lwoff (104, 105) at one time entertained the belief, in agreement with Verne, that at least a part of the carotenoid was synthesized by crustaceans from colorless precursors. Lwoff now shares the view, however, that zoosynthesis of carotenoids *de novo* has not been demonstrated with finality (personal communication, 1946).

Carotenoids are absorbed by *Carcinus maenas* directly from the food, and subsequently stored in the hepatopancreas. In males and nongravid females the pigments remain there, pending regular supplies thence to the hypoderm, but in laying females the storage organ becomes pale as the carotenoids are transported by the blood to the ovary (1, 41). Reserve supplies of carotenoids, persisting in the hepatopancreas even after some weeks of subsistence upon a carotinoid-free diet, are mobilized to the hypoderm and other tissues of *Carcinus* (2). Carotenoid proteins from the hepatopancreas appear also in the feces of *Carcinus* for some time after the crabs have been deprived of a dietary source of the pigments, but eventually the blood and hepatopancreas lose all carotenoid, and the feces become colorless (42, 43).

Quantitative investigations by Brown (13) have demonstrated losses in carotenoid in the shrimp *Palaemonetes vulgaris* when the animals are maintained upon white backgrounds, while similarly fed shrimps in brown or black colored surroundings maintained or even underwent apparent gains in their supplies of pigment. In this connection, it may be mentioned that accelereted losses in xanthophylls were found by Sumner & Fox (163) to occur in the greenfish *Girella nigricans*, but not in other species, e.g., *Fundulus parvipinnis* and *Gillichthys mirabilis* (162), when such animals were kept for extended periods in white containers. Such findings provide no proof, however, that carotenoids are synthesized by the animals, but suggest merely that environmental photic conditions influence in some way the rate or extent of assimilation or retention of dietary carotenoids. Egg-laying (leading to losses of pigment from the body), the chemical consumption of other stored materials with a temporary sparing of carotenoids, and finally factors such as cannibalism, resulting in potential gains of pigment by the predators, are considerations which cannot be neglected in such studies as Brown conducted with the shrimps.

The red acidogenic compound astaxanthin (3-3′-dihydroxy-4-4′-diketo-β-carotene) abounds in Crustacea, and was first isolated as its derivative astacin (3-3′,4-4′-tetraketo-β-carotene) from the brownish black chromoprotein of the shell, the red complexes of the hypoderm and the blue-green pigment of the eggs of the crayfish *Astacus gammarus*, as well as from the eggs of the spider-crab *Maja squinado*, by Kuhn & Lederer (84) and Kuhn *et al.* (85), and from a series of other crustaceans by Fabre & Lederer (39, 40). The green astaxanthin-protein complex from the eggs of the lobster *Homarus americanus* has been shown to possess a range of color stability between pH 4 and pH 8, and to have an isoelectric point close to pH 7; its approximate molecular weight is 300,000; its absorption spectrum shows maxima at 640 mμ and 470 mμ. This "ovoverdin" may be reversibly dissociated into its constituent carotenoid and protein moieties by heating to moderate temperatures for short intervals in the presence of neutral salts, even in the absence of air (152, 153).

A blue carotenoid-protein system was encountered in the eggs of two species of goose-barnacle, *Lepas fascicularis* and *L. anatifera* (?) by Ball (7). This compound exhibits the same thermal dissociability as was observed in pigment from the green eggs of the lobster. Ball also produced a similar reversible dissociation by careful acidification of chilled systems of the chromoprotein in the presence of ammonium sulfate.

Sørensen (150) shares the general belief that crustaceans are incapable of the biosynthesis of astaxanthin *de novo*, but considers the pigment to be an oxidation product of β-carotene or of certain xanthophylls of the diet. This view seems to be the correct one, and applies in all probability to similar pigments in coelenterates, sponges, mollusks, echinoderms, and other invertebrates. The common occurrence of acidic or acidogenic carotenoids among many invertebrate animals suggests a unique ability of such organisms to carry out partial oxidation of commoner polyene molecules without actually splitting them.

Insects.—In view of the great numbers and prominence of insects, it is perhaps somewhat surprising to find that there has not been more attention devoted to the occurrence and metabolism of carotenoids in this colorful class.

Palmer and Knight (127) found, many years ago, that yellow carotenoids are transferred from leaves, consumed by the larvae, to the hemolymph of the potato-beetle *Leptinotarsa decemlineata*, and hence to a predaceous hemipterous insect *Perillus bioculatus*, which consumes the eggs and sucks the golden yellow lymph from larval and adult beetles.

Carotenoids, transferred by the honeybee *Apis mellifera* to both honey and wax, are derived chiefly from the pollen which is consumed (145, 188). A number of carotenoids, including a lutein ester and β-carotene, have been isolated by Tischer (168) from propolis (bee-glue) which the insects derive from pollen. Certain species of ants reportedly deposit carotenoids in their eggs (37).

Przibram & Lederer (131) found α- and β-carotene in the walkingstick insect *Dixippus morosus*, and carotene in the green mantis *Sphodromantis bioculata*, but not in brown variants of the same species, even if fed carotene-rich diets. In *Phyllium pulchrifolium* Przibram & Lederer detected carotene in all stages of metamorphosis, but no xanthophylls in any of the above-named species. From the red wings of *Oedipoda minuta*, however, β-carotene and a capsanthin-like xanthophyll were recovered.

The clover-eating *Colias philodice* gives rise to a dominant larval mutant which owes its green color to the presence of dietary carotenoids, accompanying the blue degradation product of chlorophyll which occurs also in the carotenoid-free blue recessive. While the green mutants fall prey to birds less frequently than do the blue ones, because of the protective coloration of the former against the green foliage, both variants are parasitized by a hemipteran insect *Apanteles flaviconchae.* The latter predators ultimately spin yellow or white silk in their cocoons, according to whether they have preyed upon the green or the blue larvae respectively (58).

Certain insects are able to subsist upon diets entirely lacking in carotenoids or vitamin A. Examples are the flour-beetle *Tenebrio molitor* (166), the clothes-moth *Tineola biseliella* (22) and the cockroach *Blatella germanica* (11, 119). Such animals yield no carotenoids from their extracted tissues.

Uda (170), Gerould (58), Manunta (108 to 111) and others have given special attention to the genetic aspects of the silkworm *Bombyx mori* and its ability to spin yellow silk, containing carotenoids, or white silk, lacking them. One gene seems to be necessary for achieving carotenoid pigmentation of the blood and serigenous gland from alimentary sources, while a separate factor controls the ability to secrete the carotenoid in the silk.

The relatively rich supplies of carotenoids in the elytra of the lady-beetle *Coccinella septempunctatum* seem to be variable in nature depending perhaps upon the pigments derivable from this insect's consumption of aphids, which in turn receive their supplies of carotenoids from a plant host (92).

CHORDATES

Tunicates.—The major contribution on the conspicuous pigments of many simple and compound ascidians is that of Lederer (89, 92), who concentrated on four species, viz, the two solitary forms *Halocynthia papillosa* (= *Cynthia papillosa*) and *Microcosmus sulcatus*, the "social tunicate" *Dendrodoa grossularia* and the compound species *Botryllus schlosseri*. From the dark red tunic and orange internal organs of *Halocynthia papillosa* were obtained rich yields of astacin, moderate quantities of a new xanthophyll, cynthiaxanthin, and traces of α- and β-carotene. The violet-cloaked *Microcosmus sulcatus* was found to contain much free and esterified xanthophyllic material and smaller quantities of α-carotene and echinenone. Cynthiaxanthin or zeaxanthin, lutein, and fucoxanthin were suspected among the xanthophylls.

Like *Halocynthia papillosa*, the violet-red or rose-colored social ascidian *Dendrodoa grossularia* was found to contain much astaxanthin, accompanied by smaller amounts of xanthophylls and traces of α- and β-carotene.

The brown-red compound tunicate *Botryllus schlosseri* seemed to exhibit considerable variation in kinds and amounts of carotenoids. Lycopene and β-carotene were found, and capsanthin, capsorubin and pectenoxanthin were occasionally present. Such pigments as capsanthin and capsorubin were believed to be derived from the animals' consumption of pimento pepper wastes which were dumped into the harbor habitat.

The presence of heavily oxygenated carotenoids, e.g., astaxanthin, in numerous invertebrate species suggests a flexibility in the metabolism of dietary carotenoids which insects and vertebrates, save perhaps for some fishes, have largely lost.

Fishes.—The most conspicuous skin-colors in the vertebrates are undoubtedly to be found among the fishes. Numerous bright red fishes store astaxanthin or similar pigments which are probably derived from the consumption of invertebrate animals. Examples are the flesh of the salmon species *Salmo salar* (35, 38) and *Onchorhynchus nerka* (6), the scythe-fish or oar-fish *Regalecus glesne*, whose liver yields a red oil, and *Cyclopterus lumpus*, both sexes of which seem to mobilize astaxanthin from liver to skin and flesh during the summer spawning period (143). Lederer (91, 92) encountered rich stores of astaxanthin in the red skin, gill- and mouth-mucus, iris and sclera of the marine dorado *Beryx dedactylus*. The red variety of the common goldfish *Carassius auratus*, some but not all varieties of the freshwater perch *Perca fluviatilis*, and the rock cod *Sebastes marinus* likewise yield astacin (92). The sea-devil or angler-fish *Lophius piscatorius* contains astaxanthin and taraxanthin-like xanthophylls in the liver-oil (19, 149), while the former acidogenic pigment has likewise been reported in the flesh of trout (151) and accompanying α-carotene in the oily orange liver of the sunfish *Orthagoriscus mola* (148).

Many other species of fish contain no astaxanthin or other acidogenic carotenoids in any of their tissues. Some specimens of the freshwater perch *Perca fluviatilis*, for example, yield no astaxanthin, but traces of carotenes and three xanthophylls. One of these shows a single absorption maximum at 510 mμ in carbon disulfide, thus resembling astacin, but differing from the latter in being neutral (92).

The red fins of the pike *Esox lucius*, the yellow-spotted skin of the eel-pout *Lota lota* and the ovaries of *Eleginus navaga* contain no astaxanthin but copious other xanthophylls and traces of carotenes (92). Taraxanthin-like pigments are very commonly encountered in various tissues of fishes (44, 92), including the eyes (179), where they may perhaps serve to increase visual acuity by reducing chromatic aberration and glare or dazzle (183).

A few investigations have been made relative to the sources and metabolism of carotenoids in fishes (44, 162, 163, 164, 185). The Pacific killifish *Fundulus parvipinnis*, the greenfish or opal-eye *Girella nigricans*, the long-jawed goby *Gillichthys mirabilis*, the garibaldi or marine goldfish *Hypsypops rubicunda*, and the surf-perch *Cymatogaster aggregatus* contain in their epidermal xanthophores no carotenes or acidogenic carotenoids, but only esterified xanthophylls of the taraxanthin class.

In *Fundulus* the female transfers free xanthophyll to her ripening eggs, while the sexually mature male undergoes a conspicuous and measurable enrichment of its integumentary carotenoid. When maintained for extended periods upon white, yellow, red or black backgrounds, these fishes adapt themselves chromatically, tending to match the color of their surroundings. But, even when kept for weeks or months under such conditions, or when maintained in total darkness for similar periods, the animals retain in their skins essentially the same quantities of carotenoids. When maintained for fourteen weeks upon basic diets to which had been added either (*a*) the taraxanthin-like skin-xanthophyll, or (*b*) carotene but no xanthophylls, *Fundulus* was found to deposit additional integumentary xanthophyll; when receiving a diet lacking carotenoids over the same interval, the fishes underwent no gain or loss in total carotenoids. This species thus seems to demonstrate an ability to oxidize carotene to xanthophyll, and to stabilize its xanthophyll stores against metabolic oxidation.

Gillichthys mirabilis demonstrates the same maintenance of xanthophylls as does *Fundulus*, when kept in tanks of various colors. *Girella nigricans*, however, loses its integumentary xanthophyll when kept in laboratory aquaria. Such losses have been found to occur more rapidly in specimens living on white backgrounds than in others kept in black or even in yellow containers, when all food and incident light from above are standardized.

Cymatogaster aggregatus, feeding upon red shrimps (*Hippolyte californiensis*), assimilate the xanthophyll from this source, but reject quantitatively the carotenes and acidogenic carotenoids, although esters of the latter are hydrolyzed in the gut. Only a certain proportion of the alimentary xanthophyll is stored in the skin of this species, where it is re-esterified and maintained at a constant level in sexually inactive specimens. Some of the xanthophyll which has been absorbed from the gut, in excess of that which may be destined for storage in the skin or elsewhere, accumulates temporarily and in the unesterified condition in the rectal tissue of the gut, to which it imparts bright orange colors.

Amphibians.—Carotenes and xanthophylls have been extracted from the skin of the frogs *Rana temporaria* and *R. esculenta* by van Eekelen (171) and from skin, liver, kidneys, lungs, ovaries, eggs, oviducts, testes, and fat-bodies of summer and winter frogs by Rand (133). Brunner & Stein (18) and Zechmeister & Tuzson (190) found, in agreement with Rand (133), that, although there are highly variable quantities and ratios of β-carotene and xanthophylls, such as lutein, in various tissues, the carotenoid content is highest in the fat-body. Zechmeister & Tuzson isolated from 491 livers (1.35 kg. fresh weight) of *Rana temporaria* 8 mg. of pure β-carotene, small amounts of α-carotene and 60 mg. of lutein and zeaxanthin combined.

Beatty (8), studying the carotenoids of the blind and nearly colorless salamander *Proteus anguineus* from dark underground caves of North Italy and Yugoslavia, found β-carotene and small amounts of xanthophyllic pigment, but no esters of the latter. The xanthophylls were found in the body proper (minus viscera) while the liver carotenoid was nearly all carotene.

Zechmeister (187) places the frog in a class with man as representative of animals exercising little if any selection between the hydrocarbon and alcoholic types of dietary carotenoids, in contrast to the horse, which assimilates only carotenes, the hen, in whose tissues only xanthophyllic carotenoids are to be found, and the pig, whose lipids, blood and other tissues contain no carotenoids.

Reptiles.—Carotenoids are present in the skins of many snakes, lizards and tortoises. although relatively few reptiles have been examined for such pigments. Carotenoids are among the several pigments involved in the mobile homochromy of color-changing lizards such as the "Florida chameleon," actually an iguanid lizard, *Anolis carolinensis*, discussed by von Geldern (178), and an African species of chameleon shown by Manunta (110) to contain some 2 mg. of xanthophylls per hundred grams of skin, accompanied by much less free xanthophyll and minor quantities of carotene. The eggs, however, yield much free xanthophyll of the lutein class, but no xanthophyll esters and mere traces of carotene. The liver is reported to be richest of all tissues in carotenoids, containing about 10 mg. per cent; half of such pigments appear to be free xanthpohylls, a third carotenes, and the final fifth xanthophyll esters.

A carotenoid resembling γ-carotene (or rubixanthin or gazaniaxanthin) and another compound not unlike an ester of taraxanthin have been recovered from the integument of the Japanese turtle *Chrysemys scripta elegans;* an additional xanthophyll was found in the viscera (92). From the skin of *Chrysemys* terrapins in this country, Kritzler (80) extracted considerable quantities of a red xanthophyll which is distinct from lutein and shows absorption maxima in carbon disulfide at 505, 475 and 450 mμ.

The present writer has extracted from the hard, waxy, corn-grain-shaped, yellow-brown kernels from the femoral pores of the spiny-tailed iguana *Ctenosaura acanthura*(?) an esterified xanthophyll resembling taraxanthin, doubtless derived from the vegetable diet of this reptile.

Birds.—Concerning the carotenoids of the avian class there exists a very extensive literature, so that only certain outstanding contributions can be considered. Birds contain carotenoids in their liver, eyes, adipose tissues, serum, skin, eggs, and frequently in feather materials.

Palmer and his colleagues (125) demonstrated many years ago the fact that the yellow fat, skin and egg-yolk of the White Leghorn fowl are colored by dietary xanthophylls but contain essentially no carotenes. However, hens require vitamin A, and manufacture this from dietary carotene, subsequently storing part of the vitamin in the eggs (4). During the laying season, the xanthophylls are deposited in the egg-yolks instead of in the skin of legs and other areas. It has been demonstrated by numerous workers that various dietary xanthophyllic carotenoids, notably capsanthin from red peppers and zeaxanthin from yellow corn, are stored in skin and in yolk (14 to 17, 72, 74, 121, 169).

Carotenoids have been found in the iris of several breeds of domestic fowl (73), and in the retina as well, chicken retinal carotenoids including a lutein-like xanthophyll, a yellow-green carotene resembling sarcinene, and astaxanthin (181, 182).

Lönnberg (96, 100) found carotenoids in the eyes of twenty-two species of wild birds belonging to widely different orders, and in the skin of feet, bill, or face of fifteen other species.

The amber-colored oil stored in the proventriculus of the pelagic, surface-feeding fulmar petrel *Fulmarus glacialis* has been reported to contain no free or esterified xanthophylls or acidic carotenoids, but carotenes accompanied by rich stores of vitamins A and D (139). If such an interesting biochemical partition is indeed a fact, the oil and its contained carotenoid material must represent a secretion by the bird, rather than an undigested residue. Even so, it is difficult to visualize how the oil should fail to extract some of the carotenoid material from fresh food swallowed by the bird, and thus accumulate alcoholic carotenoids.

Certain birds may effect conversion of common alimentary carotenoids to colored compounds of altered constitution. The canary *Serinus canaria canaria*, for example, has been shown by

Brockmann & Völker (12) to store lutein itself in the liver, fat and egg-yolk, but to transform the pigment into a new, taraxanthin-like xanthophyll before secreting it into the new yellow feathers. Zeaxanthin is assimilated and stored by the same species, partly altered and partly unchanged, in yolk and feathers, while violaxanthin is altered in the digestive tract, but is not assimilated in any tissues or in feathers. Dietary β-carotene and lycopene were reported not to have been stored as such in tissues or in feathers.

Astaxanthin or a similar carotenoid has been encountered in the egg-yolk of the laughing gull *Larus ridibundus* and of the stork *Ciconia ciconia*, unaccompanied by any traces of carotene or lutein (12). Astaxanthin has also been demonstrated in flamingo fat (112).

Test (167) has investigated the carotenoids in the scarlet feathers of the woodpecker *Colaptes cafer*, the yellow plumes of the related species *Colaptes auratus*, and the intermediately orange-colored plumage of a suspected hybrid between the former two species. In general, three types of carotenoids prevailed in the three forms studied: (a) yellow xanthophylls, free and, to a minor extent, esterified, (*b*) α-carotene and probable isomers of this, and (*c*) unknown red, neutral epiphasic and hypophasic carotenoids exhibiting single absorption maxima. The feathers of *C. auratus* owe their yellow color principally to the presence of taraxanthin-like xanthophylls and traces of carotenes, notably the α-isomer. The scarlet hues of *C. cafer* are produced chiefly by the unique red, spectroscopically single-banded carotenoids, accompanied by some yellow xanthophylls and orange carotenes. *C. cafer* possesses a greater number of plumage carotenoids than does *C. auratus*. The predominating red color of the former species results from the presence of additional red carotenoids rather than from an actual replacement of the yellow type. Intermediately colored feathers from the orange, suspected *cafer-auratus*, hybrids contain all three classes of carotenoids encountered in the other species, but the red carotenoids in the case of the "hybrid" constitute a smaller proportion of the total than in *C. cafer*.

It has been found by Kritzler (80) that the display plumages of nuptially colored male bishop birds (*Euplectes* spp.) are rich in several carotenoids, while the henny eclipse feathers, to which the males revert after the postnuptial moult, are nearly devoid of this class of pigment. From the plumes of wild *Euplectes franciscanus*, *E. orix* and *E. nigroventris*, and from the head-feathers of the woodpecker *Melanerpes erythrocephalus*, Kritzler extracted two unfamiliar nonacidic red carotenoids and a yellow xanthophyll resembling lutein. Notwithstanding the maintenance of postnuptial males, showing their eclipse plumage, upon carotenoid-free diets for some three months, Kritzler found rich stores of residual carotenoids in liver and body-fat. When injected with pregnant mare serum, *Euplectes afra* and *E. nigroventris* mobilized such stored carotenoid pigment to new display feathers which grew in replacement of plucked henny plumage.

There is manifestly a high degree of flexibility in the complex carotenoid metabolism of the avian class. Extensive investigations into the comparative biochemical aspects of this field are clearly indicated as important future undertakings.

Mammals.—While horses and cattle, typical herbivores, store carotenes in their body-fat, liver, adrenals, corpus luteum, serum, and milk, and while man, an outstanding omnivore, carries an assortment of carotenoids in the same tissues and secretions, depending on the diet, nevertheless mammals as a class are relatively poor in this type of biochrome.

The chief carotenoid in the tissues and milk-fat of cattle is β-carotene (126), which may be accompanied by traces of α-carotene, lycopene, lutein, and cryptoxanthin (60, 61, 62). Whole ovaries of cattle are four times as rich in carotene as are testes [e.g., 0.3 mg. as compared with only 0.08 mg. per cent (187)], while the corpus luteum and corpus rubrum of the ovary may yield quantities amounting to 6 mg. and 120 mg. per cent respectively (83). Cows' plasma may contain from three to fivefold the amounts of carotene found in bulls' plasma (60), thus reflecting the greater metabolic turnover of carotene in the female (146). Vitamin A and carotenoid pigments have been obtained from the yellow patches of olfactory tissue in the upper part of the nasal cavity of cattle (120).

The blood of sheep, an antelope, and a deer were found to contain lower concentrations of carotene and vitamin A than did that of a range cow (128), while, in India, buffalo butter-fat has been found to involve only about one-tenth the concentration of carotene present in cows' butter, i.e., 0.02 to 0.035 mg. as contrasted with 0.2 to 0.57 mg. per cent respectively (6a).

The horse has been established as a typical carotene-assimilating, xanthophyll-rejecting animal, the elimination of xanthophylls occurring before such compounds can enter the general circulation through the intestinal mucosa (188, 189, 192).

Although swine consume carotenoid-rich food and require vitamin A in their ordinary and reproductive metabolism (69), they probably store the least carotenoid material of all mammals so far investigated. Even their adipose tissues contain less than 0.1 mg. per kg., following an extended diet very rich in such pigments. The liver may yield from one-fifth to one-tenth of the above quantity (191).

Astacin may be recovered in considerable quantities from the liver oil and feces of whales, which derive this carotenoid from consuming vast quantities of "krill" or small crustaceans (28, 144).

Pease (129) and Willimott (184) encountered a recessive factor in the rabbit *Lepus cuniculus* which permits the deposition of xanthophyll in the adipose tissues of certain strains of this normally "white-fatted" animal. Willimott suggested that the dominance of the "white-fatted" variant might be due to the presence of a thermolabile oxidative system in the liver, the recessive "yellow-fatted" animals lacking such an enzyme, and therefore storing rather than destroying the dietary xanthophyll.

SEDIMENTS

The high proportion of carotenes relative to xanthophylls in certain muds of the ocean floor, in contrast to the reverse condition which prevails in the green plants and the suspended detritus of the sea, may be due in considerable part to the xanthophyll-assimilating, carotene-rejecting propensities of the majority of marine animal species and in part to the biochemical reducing properties of microorganisms (52).

INDOLIC PIGMENTS

Indolic pigments, containing the familiar indole or phenopyrrole nucleus, are among the ultimate catabolic degradation products of the amino acids tyrosine, phenylalanine, and tryptophane. In this class of biochrome are included the blue, red, or purple indigoids and the various more complex yellowish, ruddy, brown, or black melanins.

INDIGOIDS

Indican, or potassium indoxyl sulfate, may be detected in the urine, notably that of herbivores such as horses and cattle. It may also occur in relatively large amounts in human cases of hepatic carcinoma. It is demonstrated by mild oxidation in acidic solution to yield the blue, chloroform-extractable compound indigo. Indigo blue itself, likewise indigo red, are encountered in microgranular form in some pathological urines.

Purple secretions of certain gastropod mollusks, e.g., *Mitra*, *Murex* and *Purpurus*, have been known since very ancient times, and the 6-6′-dibromindigo which constitutes the chief pigment has been employed as a fabric dye. In *Purpurus lapillus* the pigment arises or accumulates in the so-called adrectal or hypobranchial gland, a pale yellow strip of tissue lying along the rectal segment between this and the gill, and attached near the end of the gut (29 to 34, 95).

The simplest indole pigment is the red 5,6-quinone of 2,3-dihydroxyindole-2-carboxylic acid. It constitutes an intermediate link in the formation of melanin (134), and occurs also in the integument of the marine annelid worm *Halla parthenopoea costa*, whence it derives its common name of hallachrome. It is easily reducible and has been considered by Friedheim (55, 56) to be an accessory respiratory catalyst, notably in the oxygen consumption of unfertilized sea-urchin eggs and mammalian erythrocytes. Confirmatory investigations of this singular quinone will be of interest and must precede any serious consideration of Friedheim's theory as to its physiological role.

MELANINS

These biochromes are undoubtedly the most widely distributed of all animal pigments, and give rise to the various shades of black, gray, brown, ruddy, tawny, and Tyndall blue. Different hues arise from the fact that the responsible melanin may exist in various stages of oxidation, in different degrees of physical aggregation, and often in diverse relationships with other pigments. Widely different animal phyla share the common biochemical property of catabolically deriving melanin through enzymic oxidation of tyrosine or related phenolic compounds.

Various colored melanins are present in the ectoderm of certain coelenterates, e.g., dark variants of the plumose anemone *Metridium senile* (48), in the integument of some holothurians and ophiuroid echinoderms (174) and flatworms (21), in the epidermal melanophores of numerous reptiles, amphibians, fishes, and cephalopods, and notably in the specialized anal gland (ink-sac) of the latter. The ink-gland was described long ago by Gessard (59), who also demonstrated the enzyme tyrosinase in melanin-free glandular tissue from fresh animals, as well as in the dried *Sepia* sacs of commerce.

Among vertebrates, melanins are encountered not only in dermal and epidermal tissues, but also in such integumentary products as hair, feathers, and scales. Internal connective or other membranous tissues, e.g., choroid, peritoneum, pia mater etc., of numerous fishes, amphibians, reptiles, and birds likewise contain black melanin.

The onset of melanization in the integument of insects seems to be associated with any of several metamorphic, stages, e.g., the newly hatched larvae of the cockroach *Phyllodromia germanica* (130), the pupating larva of the fly *Musca carnaria* (25), and in the developing caddis-fly *Limnophilus flavicornis* at the end of the larval period and in the late nymphal stage, but not in the adult (138). The integument of the developing "meal-worm" beetle *Tenebrio molitor* is heavily invested with melanin soon after the process of shedding from the pupal stage has been completed. Pupae of the locust *Tibicen septendecem* show a rapid cuticular melanization on emergence from their seventeen-year residence underground (63, 64).

Lea (87) claims that ascorbic acid, an easily oxidizable compound, inhibits the enzymic oxidation of tyrosine to melanin. He also demonstrated an acceleration of melanogenesis following depression of the normal physiological sodium chloride level.

Fresh human epidermis has been found by Rothman *et al.* (141) to contain water-soluble sulfhydryl compounds, absent in the corium, which inhibit melanogenesis in tyrosine-tyrosinase systems. Rothman and his colleagues suggest that the inhibitory SH compounds may be oxidized or otherwise altered by such melanogenic stimuli as sunshine, x-rays, etc., whereupon the enzymic "tanning" process takes place readily.

Physiological attributes of melanized insect-cuticles have been suggested as follows by Kalmus (76, 77): (*a*) increased protection against short-waved injurious light rays, (*b*) increased rate of heat exchange, (*c*) enhanced toughness or mechanical resistance, (*d*) decreased wettability, and (*e*) protection from desiccation.

The Silky cock, bearing white feathers but black skin, mesenteries, periosteum, pia mater, and connective tissues, transmits this melanistic pattern, when bred to a melanin-free hen, only to his daughters (132).

According to Rawles (135), melanogenic skin may be grafted from embryonic robins to the wing of the developing White Leghorn chick embryo, resulting in temporary melanization of the down growing from the transplant in the hatched host. The robin's melanophores, having migrated from the graft into the host's feather-germs, express the ruddy color until moulting, the graft thereafter bearing host-colored (white) feathers.

It has been demonstrated by Vilter (176, 177) that axolotls (*Amblystoma mexicanus*) generate more melanin and greater numbers of melanophores when living upon black backgrounds than when maintained in white surroundings. Similar observations have applied to frogs (*Rana temporaria*) by Dawes (23, 24) and to fishes, e.g., the Atlantic killifish *Fundulus heteroclitus* by Odiorne (124), the guppy *Lebistes reticulatus* by Sumner & Wells (165), the long-jawed goby *Gillichthys mirabilis*, the mosquito-fish *Gambusia patruelis*, and the greenfish *Girella nigricans* by Sumner and his colleagues (159, 160, 161).

Sumner (156, 157, 158) provided incontrovertible experimental evidence for the survival value of melanistic chromatic adaptation of fishes in the direction of concealment against attack by various predators.

Red hair from the human head contains, according to Rothman & Flesch (140) a red, iron-containing, acid-soluble pigment not found in other human or nonhuman hair. The same pigment, or a closely similar one, has been isolated by Nickerson (122) from red poultry feathers, and has been found to be derivable from the oxidation of black melanin.

SCHEMOCHROMES

While the blue colors of numerous coelenterates, nudibranch mollusks, crustaceans, echinoderms, and other invertebrates are due to the presence of acidogenic carotenoids conjugated with protein, equally arresting blue hues, occurring in the skin of numerous fishes, reptiles, some primates and the skin and feathers of many birds, arise from a very different principle. It involves reflection of the scattered short-waved (blue and violet) fractions of incident light by very fine particulate bodies of mean diameter lying between about 0.4 and 0.7μ, while the longer-waved components (yellow, orange, and red rays) penetrate the layers containing these light-scattering inhomogenieties and are absorbed by deposits of melanin situated beneath. Without the underlying absorbing screen of melanin, the blue colors would not appear (113, 114). These so-called "schemochromic" blues of Tyndall scattering are observable in the blue sky, in blue smoke, which casts a complementary reddish shadow, and in various opalescent systems, such as agar-gel, placed against a black surface.

Examples of Tyndall blues in the biological realm could be multiplied at great length, but may be confined to a very few for present purposes, e.g., the brilliant blue spots on the skin of the young garibaldi *Hypsypops rubicunda*, in the tail and belly of the blue-tailed skink *Eumeces skiltonianus*, in the facial and neck-skin of such birds as the turkey, guinea-fowl, and double-wattled cassowary *Casuarius galateus*, in the muzzle, scrotum and buttocks of such primates as the West African drill *Cynocephalus leucophaeus* and the mandrill *Papio sphinx*, and in the blue eyes of man, kittens, and some monkeys.

The blue colors of feathers arise from the presence of countless minute air-vesicles within the so-called box-cells overlying deposits of melanin in the barbs (53, 54, 66, 67, 68, 113). Replacement of the air in such a scattering system, by a foreign fluid, e.g., phenol, whose refractive index approaches that of feather-keratin (1.54) causes a complete discharge of the blue color, which is readily restored by leaching out the foreign fluid. Destruction of the melanin layer by oxidation with hydrogen peroxide extinguishes the Tyndall effect, but this may be restored by painting the underside of the feather-barbs with India ink.

Countless manifestations of brilliant iridescence and "metallic" colors are present in insects' cuticles, feathers of peacocks, hummingbirds, etc., and arise from the interference of reflected light-waves by very thin laminations, backed beneath by deposits of melanin, which absorb the penetrating rays, thus rendering the reflected portion the more pure in its series of Newtonian colors (5, 114 to 117, 136, 137, 155). Removal of the melanin layer greatly diminishes the visible iridescence, which may be restored by substituting a black paint, such as India ink.

In black, Tyndall blue or iridescent feathers, the melanin involved is still to be regarded as but a catabolic by-product, discharged by integumentary cells.

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Scripps Institution of Oceanography
University of California
La Jolla, California

Contribution No. 326

Bacterial Release of Oil From Oil-Bearing Materials

By DR. CLAUDE E. ZoBELL

Associate Professor of Microbiology at the Scripps Institution of Oceanography of the University of California, and Director of API Research, Project 43A.

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THE ABILITY of certain bacteria to liberate oil from oil-bearing sands under certain conditions may point the way to a wider understanding of the phenomena underlying the accumulation or formation of hydrocarbons in reservoirs. Study of such bacterial action may point the way to ultimate recovery of a large portion of oil now left in place. The author describes the experiments carried out to define basic principles of bacterial action under conditions simulating those of the oil reservoir. The findings given offer basis for continuing research, and clarify existing limitations.

PETROLEUM hydrocarbons, most of which are virtually insoluble in water, are generally rendered more susceptible to microbial attack by adsorbing them on sand, glass wool, asbestos fibres, diatomaceous earth, or other solid surfaces.[86] In experiments designed to compare the effectiveness of various inert absorbents for dispersing hydrocarbons in bacterial cultures, it was observed that certain bacteria liberated paraffin oil from sea sand and other solids on which the oil had been absorbed.[76] A film of oil appeared on the surface of mineral salts solution in which the bacteria were growing, whereas little or no oil separated from the adsorbents in uninoculated controls.

The liberation of oil was also observed from samples of Athabaska tar sand covered with nutrient solution in which sulfate-reducing bacteria were growing. Further experiments have conclusively demonstrated the ability of bacteria to liberate oil from oil-bearing sands under certain conditions, and a few observations have been made on the mechanism by which bacteria release oil from solids.[75] It is the purpose of this paper to summarize some of these observations.

Experiments With Athabaska Tar Sand

Athabaska tar sand consists of an agglomeration of fine sand impregnated with a heavy, black, viscous tar, little or none of which is removed by water at ordinary temperatures. From 12 to 20 grams of crude oil or tar, having a density of about 1.12 (—5-degree API gravity), can be extracted per 100 grams of the tar sand with petroleum ether, pentane, carbon tetrachloride or similar solvents.

While testing samples of Athabaska tar sand for their effects on the growth of bacteria, it was noted that certain cultures released oil from the sand. The multiplication of sulfate-reducing bacteria in nutrient solution covering the tar sand in glass-stoppered bottles was accompanied by the gradual separation of oil or tar from the sand. Oil droplets, apparently buoyed up by adherent gas bubbles floated to the surface of the nutrient solution in which bacteria were growing. Most of the oil settled back in a viscous layer immediately overlying the sand, but some of the released oil remained in a film floating on the surface of the nutrient solution.

Irregular shaped lumps of the tar sand ranging from one-fourth to one-half inch in diameter were slowly disintegrated by the bacterial cultures. The free sand grains spread out in a layer on the

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bottom of the culture bottle. After several days incubation at 27° C. the tar sand changed in color from black to light gray, indicating that most of the tar had been removed from the sand. Little or no oil was released from similar samples of tar sand treated with sterile nutrient solution.

The approximate density of the oil liberated from tar sand was estimated by noting its behavior in salt solutions of various densities. For example, the film of oil which floated to the surface of nutrient solution prepared with sea water (density about 1.03) and remained at the surface probably had a density of less than 1.03. This was confirmed by sending a small sample of oil decanted from the surface of the nutrient solution to the Esso Laboratories where technologists, working under the supervision of Dr. W. J. Sweeney, found that the oil separated from Athabaska tar sand by bacteria had a density of approximately 1.0. This corresponds to ten API gravity and may be compared with —5 API gravity for the original crude.

It is not to be inferred that all of the oil released by bacteria from the tar sand was lighter than the original crude. The density of most of the oil or tar separated from the tar sand by bacteria ranged from 1.10 to 1.14, corresponding to —3 degree API to —8 degree API gravity.

Composition of Nutrient Solution

In the intial experiments, samples of Athabaska tar sand were covered with a nutrient solution consisting of sea water enriched with 0.5 percent calcium lactate, 0.2 percent ammonium sulfate, 0.05 percent ascorbic acid, and 0.02 percent sodium sulfide. Sea water provides a physiologically balanced mineral salts solution.[77] Diluting it with distilled water permits the growth of fresh-water organisms, or it can be fortified with sodium chloride to provide for the growth of halophilic organisms. Lactate is a good source of energy for sulfate-reducing bacteria.[4,48] Ammonium sulfate provides both utilizable nitrogen and an hydrogen acceptor:

$$SO_4^{--} + 10H \rightarrow H_2S + 4H_2O$$

Either sulfate, thiosulfate, or sulfite appears to be essential for the growth of sulfate-reducing bacteria. Ascorbic acid and sodium sulfide deplete oxygen from the solution and help to create a low redox potential,[78] which favors the growth of sulfate-reducing bacteria. The hydrogen-ion concentration of the nutrient solution was adjusted to pH 7.5 by the addition of normal sodium hydroxide.

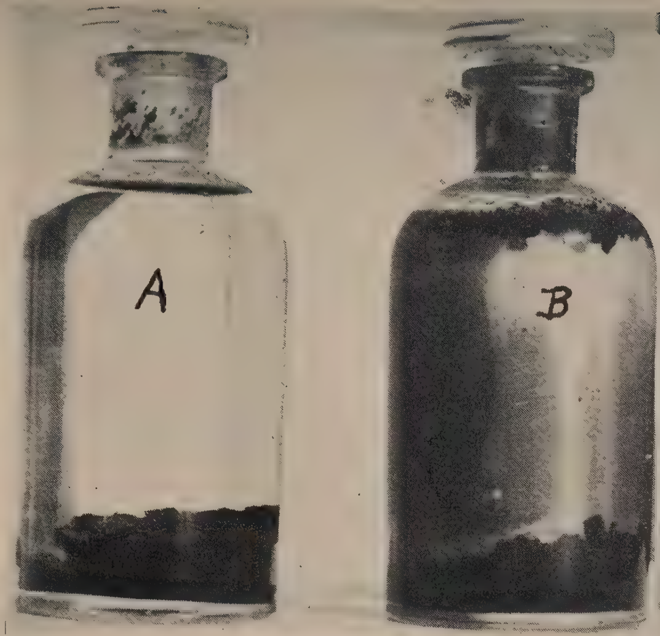
Since the growth of sulfate-reducing bacteria generally results in a decrease in the pH, in some experiments the nutrient solution was buffered by the addition of powdered calcium carbonate. The presence of calcium carbonate was found to promote the release of oil by bacteria, owing partly to its favorable buffer effect but owing mostly to the decomposition of the carbonate with the formation of carbon dioxide gas, bubbles of which tended to buoy up droplets of released oil.

Glucose, starch, cellulose, and other carbohydrates served as satisfactory substitutes for lactate as an energy source in mixed cultures containing sulfate-reducers. In fact, gas evolving from the fermentation of carbohydrates by anaerobes promoted the release of oil from samples of Athabaska tar sand, but the effect of such societies of mixed microflora on the resulting oil was quite variable. In some experiments the oil was emulsified, and in other experiments there was clear-cut evidence that much of the oil was modified or completely destroyed after prolonged incubation. The action of microorganisms on petroleum hydrocarbons has been summarized.[79]

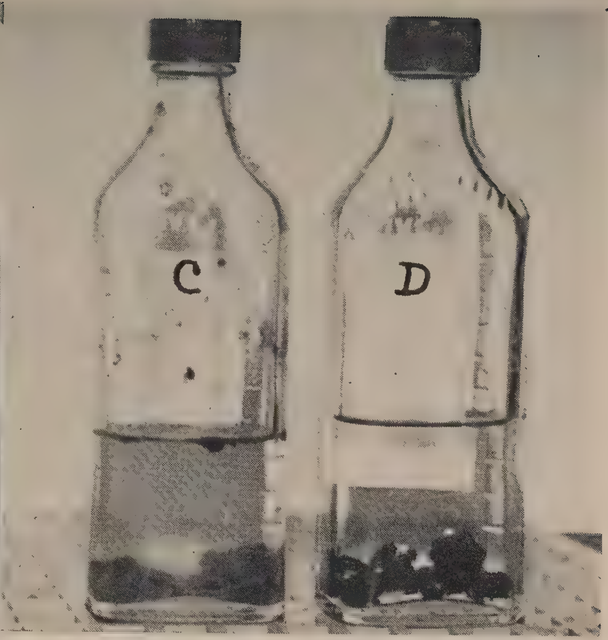
Action of Pure Cultures

Pure or partially purified cultures of sulfate reducing bacteria released oil from samples of Athabaska tar sand less rapidly than many of the mixed cultures tried. Pure cultures also had less tendency to modify or destroy the oil.

It has been demonstrated that certain sulfate-reducing bacteria attack petroleum hydrocarbons, but they do so only very slowly. Long-chain hydrocarbons in the paraffin wax range are utilized more readily than lighter hydrocarbons. It was predicted by Tausson and Aleshina[84] from thermodynamic calculations and confirmed experimentally by No-



Glass stoppered bottles containing Athabaska tar sand and mineral solution. Bottle A is an uninoculated control (no bacterial action) and bottle B shows a layer of oil released by sulfate-reducing bacteria.



Note the globules of oil on the surface of the medium and the disintegrated clumps of oily shale on the bottom of bottle C in which mixed culture of bacteria have been active, and compare with the control bottle D which contains no bacteria.

velli and ZoBell[39] that no paraffin hydrocarbon having fewer than ten carbon atoms is attacked by sulfate-reducing bacteria. Aromatic or cyclical hydrocarbons are also attacked.[66]

Certain sulfate-reducing bacteria can slowly develop on Athabaska tar sand treated with mineral solution containing no other organic nutrient, provided oxygen is excluded and the redox potential is sufficiently low. Under these conditions, oil is slowly released; much more slowly than by mixed cultures or in mineral solution enriched with lactate or carbohydrate.

After growing pure cultures of sulfate reducers for from ten to 20 days at 27° C. in mineral solution containing no other carbon or energy source than that provided by samples of tar sand, a film of oil commenced to accumulate on the surface of the mineral solution and lumps of the tar sand started to disintegrate. Within six to 12 weeks there was a fairly complete partition of the sand and crude oil, although the sand grains were still discolored with tar. In sea water medium most of the crude oil released from Athabaska tar sand remained in a black, viscous layer immediately over the sand.

Even after 12 weeks' incubation at 27° C. there was no readily discernible evidence that pure or partially purified cultures of sulfate reducers had destroyed any appreciable quantity of oil from Athabaska tar sand. Obviously, the multiplication and metabolism of the bacteria had required some carbon compound, but the amount used was extremely small as compared with the total quantity of crude present.

There are no experimental results to indicate whether the bacteria impaired or improved the quality of the oil for refining purposes. Based upon other experiments, however, it is believed that sulfate-reducing bacteria preferentially attack nitrogenous, sulfur-containing, and oxygenated compounds or long-chain hydrocarbons in the paraffin wax range, but much more work must be done to establish this point.

Oil-Saturated Shales

Appreciable quantities of crude can be removed from oil-saturated shales by extracting samples with acetone, pentane, carbon tetrachloride, or similar solvents. Water at ordinary temperatures removed little or no oil from the samples of oily shales with which we worked. Sulfate-reducing bacteria have been found to release oil from samples of Santa Maria oily shales more rapidly than from Athabaska tar sand, although the total quantity of oil released from the oily shales was not as great as the total amount released from samples of Athabaska tar sand.

Mixed as well as pure cultures of sulfate reducers grew readily in glass-stoppered bottles containing small lumps of Santa Maria oily shale and filled to capacity with nutrient medium having the following composition:

Sea water	1000.0 ml.
Calcium lactate	5.0 gm.
Ammonium sulfate	2.0 gm.
Ascorbic acid	0.5 gm.
Sodium sulfide	0.2 gm.

Growth of the bacteria was accompanied by the separation of oil from the solid sediment. Droplets of oil entrained in gas bubbles were carried to the surface of the medium. There the oil remained for a while suspended in stringy stalactites, and then it slowly settled again owing to the weight of adherent particles of sand, silt, and clay as the gas escaped. This process continued for several days, during which time small lumps of the oily shale were slowly distintegrated and the oil was gradually released from the solids. Much of the oil was emulsified in the sea water medium.

Similar results were obtained with samples of oil-saturated shale from the Casmalia area and with tar sand from the Sisquoc area near Lompoc, Calif.

No Oil From Oil Shales

Although bacteria liberated oil from tar sands and from oil-saturated shales, no oil whatever was liberated from samples of shale containing no free oil. This generalization is based upon only a few preliminary observations on samples of Chattanooga shale from Kentucky and Green River shale from Colorado. Such shales yield oil by pyrolysis but not by treatment with solvents at ordinary temperatures.

There is no evidence to indicate that bacteria can convert the bituminous material of oil shales into crude. Small lumps of the oil shale were not disintegrated by any of the bacterial cultures tried, and there is no reason to believe that oil shale may be broken down by bacterial activity. The failure of bacteria to liberate oil from oil shales containing no free oil strengthens the conviction that the bacterial release of oil from tar sands or oily shales is primarily a mechanical process, the mechanism of which will be discussed in a later section.

Bacterial cultures also failed in preliminary experiments to release oil from samples of natural rock asphalt, gilsonite, or ozocerite. Samples tested include the following:

XXIX:90-1 Vernal natural asphalt, Pope quarry, Uintah County, Utah

XXIX:90-2 Sunnyside natural asphalt, Means-Gibson quarry, Carbon County, Utah

XXIX:90-3 Gilsonite, Big Bonanza mine, Uintah County, Utah

XXIX:90-4 Ozocerite, Soldier Summit, Uintah County, Utah

XXIX:126-1 Gilsonite, Little Emma mine, Uintah County, Utah

XXIX:126-2 Gilsonite, Little Bonanza mine, Barber Asphalt Company, Utah

XXIX:126-3 Gilsonite, Cowboy vein, Barber Asphalt Company, Utah

XXIX:126-4 Manjak asphalt, Bahia Hondo mine, Pinar del Rio, Cuba

Bacteria were not inhibited by these asphaltic materials. Some of the asphaltic materials were attacked by bacteria but no oil was liberated.

Oil-Bearing Sand Cores

Cores of oil-bearing sands, two to three inches long and two or 2½ inches in diameter, have been received from Dr. R. V. Hughes, director of production research of the Pennsylvania Grade Crude Oil Association. The cores were placed in half-pint, Ball-brand fruit jars fitted with glass lids and rubber gaskets. Before sealing, the jars were completely filled with nutrient medium having the following composition:

Sea water	750.0 ml.
Tap water	250.0 ml.
Potassium phosphate, K_2HPO_4	0.2 gm.
Sodium sulfite, Na_2SO_3	0.1 gm.
Ammonium sulfate, $(NH_4)_2SO_4$	1.0 gm.
Magnesium sulfate, $MgSO_4.7H_2O$	0.5 gm
Calcium lactate	3.5 gm.
Bacto-peptone	10.0 gm.
Ascorbic acid	0.1 gm.
Sodium sulfide, $Na_2S.9H_2O$	0.2 gm.

The reaction of the medium was adjusted to pH 7.5 after autoclave sterilization.

The medium was inoculated with sulfate-reducing bacteria, Culture No. 314-2, originally isolated from Mission Bay mud.[85] The bacteria multiplied prolifically, and after nine days' incubation at 27° C. a film of oil commenced to appear on the surface of the medium covering the oil-bearing sand cores. No oil was released from identical controls held in the refrigerator at near 0° C., at which temperature bacterial multiplication was inhibited.[73] Neither was there any oil released from controls treated with 1.0 percent phenol to prevent the growth of bacteria.[84]

Oil was released from cores of oil-bearing sands as follows:

XXIX:86-1 Horizontal core from Franklin oil mine, Franklin, Penn.

XXIX:86-2 Richburg sand from Bolivar, N. Y.

XXIX:132-1 Oil-well core No. 22, Olean Coring Company, Olean, N. Y.

XXIX:132-2 Oil-well core No. 25, Olean Coring Company, Olean, N. Y.

XXIX:132-4 Oil-well core No. 55 Olean Coring Company, Olean, N. Y.

Negative results were obtained with about a like number of oil-bearing sand cores from the same general formations. Further research work, such as that being conducted by Dr. Jay V. Beck in the microbiology laboratory of the Pennsylvania Grade Crude Oil Association at Bradford, will be required to elucidate the factors which influence the bacterial release of oil from oil-bearing sands.

A slow, though quite definite, release of oil from oil-bearing sand cores from the Franklin mine has been observed in bottles filled with a purely mineral medium, lacking organic matter, inoculated with pure or partially purified cultures of sulfate-reducing bacteria. The multiplying bacteria were able to obtain their energy and carbon requirements from materials in the oil-bearing sands.

Synthetic Sediments

In order to study the mechanisms by which bacteria cause the release of oil from solids, a series of experiments has been conducted with synthetic sediments and various kinds of solids saturated with either crude oil or fractions thereof. Glass slides, glass beads, glass wool, ignited sea sand, silt, various kinds of clay, calcium carbonate, and other types of sedimentary materials have been used for this purpose. In some experiments oven-dried solids were mixed with oil and the excess oil removed with water. In other experiments the water-wet solids were mixed with oil to the point of saturation. While the amount of oil held by the synthetic sediments was influenced by the method of preparing the mixtures, bacteria seemed to release oil just as readily from water-wet as from oil-wet solids.

Certain clays and colloidal materials adsorbed oil so tenaciously that it could not be removed by treatment with either solvents or bacterial cultures. As with oil shale, however, the oil could be recovered from such adsorbents by heating in vacuo in a retort. Such observations have led the author to wonder whether oil produced by the pyrolytic treatment of oil shale occurs in shale as kerogen "bituminous" material which is converted into oil by heat or if it occurs as hydrocarbons or related compounds tightly bound to clay or colloidal particles.

Decomposition of Gypsum

Sulfate-reducing bacteria slowly decompose gypsum, anhydrite, and other inorganic sulfates. Adsorbed oil is thereby released and pore or void spaces might be formed, provided the calcium or other cation were converted into a soluble salt. The solubility of calcium salts in sediments depends primarily upon the pH.

One might think that the reduction of sulfate, a strongly acidic radical, would increase the pH, a change that would promote the precipitation rather than the dissolution of calcium. If sulfate occurs in sediments, however, in the form of gypsum, anhydrite, or other salt that is virtually insoluble in water, it would have little effect upon the pH. On the other hand, the more soluble hydrogen sulfide resulting from the reduction of sulfate is itself slightly acidic:

$$CaSO_4 + 8H + 2CO_2 \longrightarrow Ca(HCO_3)_2 + 2H_2O + H_2S$$

The hydrogen and carbon dioxide for the simplified reaction might come from the oxidation of organic matter by sulfate-reducing bacteria or from other sources. Energy for the bacterial reduction of sulfate may come from the oxidation of hydrogen[61, 71, 81] or from the oxidation of organic compounds.[4, 46] Organic compounds are oxidized to carbon dioxide or carboxylic acids with a resultant decrease in the pH of the medium. Active cultures of sulfate reducers in unbuffered media were observed by Rittenberg[46] to cause the following changes in pH:

pH Initial	pH after 14 days	pH after 35 days
7.8	6.0	5.8
7.0	6.4	5.9
6.0	5.9	5.8

In four other experiments reported by Rittenberg,[46] sulfate-reducing bacteria caused decreases in pH from an initial value of 8.5 to an average of pH 7.1 in 20 days at 30° C.

A good way to demonstrate the activity of sulfate-reducing bacteria is to introduce them into a plaster of paris medium having the following composition:

Sea water (or other mineral solution)	1000.0 ml.
Ferrous ammonium phosphate, $FeNH_4PO_4$	0.1 gm.
Plaster of paris, $CaSO_4.2H_2O$	50.0 gm.
Calcium carbonate, $CaCO_3$	40.0 gm.
Calcium lactate, $Ca(C_3H_5O_3)_2$	5.0 gm.
Ascorbic acid, $C_5H_8O_6$	0.1 gm.

Before the medium sets or solidifies, it is inoculated with material suspected of containing sulfate reducers, dispensed in test tubes. After a few days incubation the activity of sulfate reducers is indicated by the appearance of black spots or zones in the chalky white medium, caused by the reaction of hydrogen sulfide from sulfate with ferrous iron:

$$H_2S + FeNH_4PO_4 \rightarrow FeS + H_2NH_4PO_4$$

The ferrous sulfide is black.

Mineral oil has been substituted for calcium lactate in the plaster of paris medium with similar results, although sulfate-reducing bacteria grow less rapidly when dependent upon hydrocarbons as a source of energy.

Carbonates Are Dissolved

A good many bacterial species dissolve carbonates by producing organic acids. This is particularly true of anaerobes, many of which ferment carbohydrates with the formation of butyric, lactic, propionic, acetic, or other carboxylic acids. Such acids may be produced also by the anaerobic decomposition of proteins and fats.

The tendency is for bacteria to break higher fatty acids down into lower members of the series, which being more strongly dissociated in water are more acidic. The overall effect is to lower the pH of the medium in which such bacteria are growing. It is not uncommon for anaerobic bacteria to produce enough acids in unbuffered nutrient media to change the reaction from pH 7.5 to pH 6.0 or lower. The tendency is to convert calcium carbonate into bicarbonate below pH 9.5 and to convert bicarbonate into carbon dioxide below approximately pH 7.5:

$$2CaCO_3 + 2HA \rightarrow Ca(HCO_3)_2 + CaA_2$$
$$Ca(HCO_3)_2 + 2HA \rightarrow 2CO_2 + 2H_2O + CaA_2$$

where A is a monovalent acid radical.

Carbonic acid, H_2CO_3, resulting from the combination of water with carbon dioxide produced by respiring bacteria, tends to dissolve limestone and other carbonate rocks. If particles of limestone, dolomite, or other carbonate materials, to which oil is adsorbed, are dissolved, the adsorbed oil is liberated. Simultaneously, void or pore spaces are formed which provide for the accumulation or migration of oil. The tendency of bacteria to dissolve carbonates is believed to be one of the principal mechanisms by which they contribute to the liberation, migration, and accumulation of oil in sedimentary materials. Certain sulfate-reducing bacteria are endowed with this ability.

Hydrogen-oxidizing bacteria may also help to dissolve limestone or dolomite. Molecular hydrogen, which serves as a source of energy for such bacteria, may be produced during the anaerobic fermentation of organic matter,[81] it may result from the effects of radioactivity on hydrogen-containing compounds,[50,51] or hydrogen may be formed from any one of a number of other chemical reactions in the earth's crust.[28,38]

The best known of the hydrogen-oxidizing bacteria are those which reduce carbon dioxide to methane:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$$

The work of Söhngen,[54] Fischer et al,[22] Stephenson and Stickland,[63] Barker,[5,6] Buswell,[15] and others indicate that this is the principal way in which methane is formed. The utilization of carbon dioxide with the formation of methane would tend to dissolve carbonates, causing the following simplified series of reactions to proceed to the right:

$$CO_3^{--} \rightarrow HCO_3^{-} \rightarrow CO_2 \rightarrow CH_4$$

Other types of anaerobic bacteria have been described which oxidize hydrogen while reducing carbon dioxide to acetic acid:[7,23,71]

$$2CO_2 + 4H_2 \rightarrow CH_3COOH + 2H_2O$$

Propionic acid and butyric acid[8] may likewise be formed by the reduction of carbon dioxide and the oxidation of hydrogen. Acids dissolve carbonates. Whether such acid-producing bacteria are present and active in petroliferous sediments is highly speculative, but there are many reasons for believing that methane-producing[15,81] and sulfate-reducing bacteria have been active and may still be present in certain oil bearing formations.[9,24,25,26,81]

Sulfate-reducing bacteria have been found to release oil quite effectively from synthetic sediments consisting partly or entirely of oil-saturated calcium or magnesium carbonate in the presence of appropriate nutrient media.

Effect of Evolved Gases

A few bacterial species consume or fix carbon dioxide; nearly all physiologically active bacteria produce carbon dioxide. Besides its effects on the solubility or porosity of calcareous sediments, carbon dioxide may influence the release and movement of oil in other ways. Carbon dioxide decreases the viscosity of oil, thereby promoting the flow of oil. Moreover, tiny bubbles of carbon dioxide have a buoyant effect on droplets of oil or gas bubbles may force oil through capillary spaces or out of micro-traps. Reference has been made to the tendency of bacterially produced gases to promote the separation of oil from solids in laboratory experiments, although carbon dioxide may behave somewhat differently under high pressures encountered at great depths.

Methane produced by bacteria in the immediate vicinty of oil may dissolve oil, thereby rendering it more fluid or mobile. Methane, hydrogen, or other gases produced in micro-traps or pore spaces having dead ends could be expected to expel droplets of oil into central channels or reservoirs of oil. The total quantity of oil locked up in dead-end pockets or pore spaces of microscopic dimensions is probably appreciable.

Affinity of Bacteria for Solids

Many species of bacteria grow tenaciously attached to solid surfaces. This is the basis of the buried glass-slide technique of Cholodny[18] for the direct microscopic study of soil bacteria. It is also the basis of the submerged glass-slide technique employed by Henrici,[19] ZoBell and Allen,[82] Hotchkiss and Waksman,[31] Smith and ZoBell,[58] and others[74] for making ecological surveys of water bacteria. Kusnetzowa[38] believed that all water bacteria are capable of attaching themselves to glass or other inert solids. Henrici and Johnson[30] have described several species of periphytic bacteria which grow only attached to a firm substrate. Fifteen species of bacteria isolated from marine materials were found by ZoBell and Upham[87] to be forms which grew preferentially or exclusively attached to solid surfaces. Certain varieties of sulfate reducers and other kinds of bacteria have been found to have sufficient affinity for solid surfaces to crowd off films of oil or grease.

In the course of their life cycle, sulfate reducers pass through a "swarm" stage which is followed by a "resting" stage. During the swarm stage the bacteria are actively motile, but during the resting stage they settle down on and attach themselves to a solid surface, whether it be the bottom of the culture receptacle, glass beads, sand, or glass slides. The tendency of bacteria to attach themselves to solid surfaces has been studied by immersing glass slides in active cultures. After different periods of immersion the glass slides were removed for microscopic examination. Every square micron of surface was found to be coated with adherent bacteria after two or three days' immersion in culture media incubating at 27° C.

Coating the glass slides with films of petrolatum or heavy oil has proved to be no deterrent to the attachment of bacteria in culture media. Not only did the bacteria tenaciously attach themselves to immersed glass slides but in so doing they seemed to crowd off films of grease or oil. Small droplets or layers of the latter were gradualy released and appeared floating on the surface of the nutrient media.

Similar results have been observed when glass beads, glass wool, and silica sand, coated with grease or oil, were covered with bacterial cultures growing under anaerobic conditions. The release of oil is attributed primarily to a mechanical action of bacteria settling down and growing on solid surfaces, although carbo dioxide and surface tension depressants produced by the bacteria may contribute to the removal of oil or grease from solid surfaces.

Surface Tension Depressants

Soaps, detergents, or other surface-active substances tend to remove oil from solid surfaces under certain conditions.[12] There is evidence that surface tension depressants are produced by microörganisms. For example, Cooper[20] found that the tubercle bacillus reduced the surface tension of a synthetic medium from an initial value of 72.4 dynes per centimeter to 53 dynes after eight weeks. A culture of *Penicillium notatum,* studied by Reid,[42] reduced the surface tension of nutrient medium in which it was growing, from 52.6 to 43.1 dynes per centimeter. Further observations on the relationships between bacteria and surface tension of their culture media have been summarized by Larson.[34]

Pure or partially purified cultures of sulfate-reducing bacteria have been observed to reduce the surface tension of sea-water medium enriched with peptone and calcium lactate from initial values of around 63 dynes per centimeter to as low as 46 dynes after six weeks incubation at 27° C. Culture medium, containing surface tension depressants produced by bacteria, was sterilized either by treating it with 1.0 percent phenol or by heating it to 100° C. for ten minutes. The resulting bacteria-free medium, having a surface tension of around 50 dynes per centimeter, was observed to effect the release of oil from ignited sea sand saturated with oil. Since no oil was released from oil-saturated sea sand by uninoculated control medium having a surface tension of around 63 dynes per centimeter, the observation was interpreted as indicating that bacterially produced surface-active substances or wetting agents were partly responsible for the release of oil from solids.

Surface-active substances, produced by bacteria growing on solid surfaces, may play an important role in the liberation of oil from solids. Further observations along this line are indicated.

The release of oil from plant or animal tissues is another function attributed to bacteria. Most plants and a good many animals produce or store hydrocarbons in their tissues to some extent. Not infrequently such hydrocarbons may be so intimately bound by organic matrix that the hydrocarbon is not freed until the organic matrix is decomposed. The selective degradation of such organic matrices by bacteria may contribute to the liberation and accumulation of petroleum hydrocarbons, particularly in recently deposited sediments. Of course, whether the hydrocarbons will also be destroyed by bacteria will depend upon the types of bacteria present and the environmental conditions.[79]

It is a fairly common experience to note an increase in the amount of nonsaponifiable oily material that can be extracted with ether or other solvents from algae during the decomposition of the latter. This is partly attributable to the synthesis of hydrocarbons by bacteria, but probably primarily attributable to the liberation of hydrocarbons from decomposed algal tissues. The storage of the sludge of diatoms was found by Clarke and Mazur[19] to be accompanied by a fall in the free fatty acid content and a rise in hydrocarbons. Storage of such material did not always result in an increase in hydrocarbons, presumably due to differences in microbial flora. Depending upon the microbial species present and the prevailing environmental conditions, bacteria or fungi may liberate oil by the selective decomposition of the organic matrix, they may destroy oil, or they may synthesize oil.

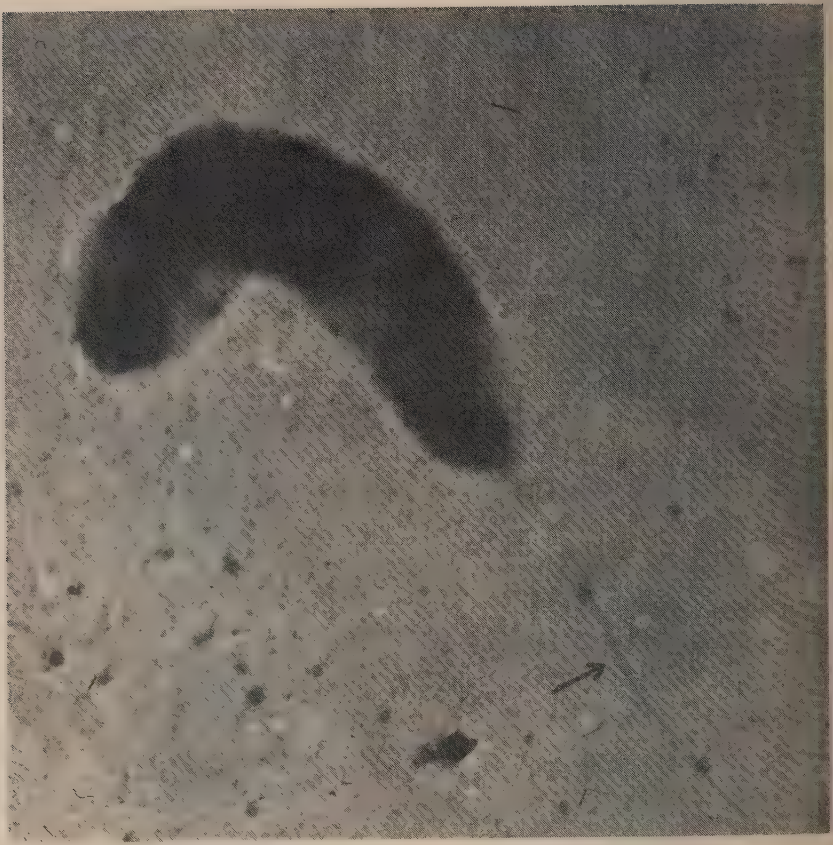
The bacterial synthesis of paraffinic hydrocarbons ranging from C_{10} to C_{25} has been reported by Jankowski and ZoBell[32] and confirmed by more recent observations. The hydrocarbons synthesized by bacteria constitute a part of the cell substance of the bacteria and can be extracted only after the death and decomposition of the bacteria.

Thiessen[68] has expressed the view that spores of various plants, remains of which are found in oil shales, consist largely of oils and waxes which are liberated only upon the decomposition of the spores. According to Stadnikow and Weizmann,[57] certain species of algae contain considerable amounts of nonsaponifiable oil and waxy material. That long-chain hydrocarbons ranging from $C_{16}H_{34}$ to $C_{37}H_{76}$ occur in the leaves and bark of many species of plants is documented by the literature summarized by Seyer,[49] Chibnall and Piper,[16] and Sanders.[47] Heptane, pentadecane, hexadecane, eicosane, and higher paraffinic hydrocarbons are common constituents of plant and insect tissues, according to Chibnall et al.[17] Sanders[47] has presented evidence that unicellular algae have contributed considerable amounts of waxy and oily substances to petroleum, as judged by decay-resistant remains of such organisms.

An enzyme preparation from microorganisms for deproteinizing rubber hydrocarbons has been described by Wallerstein.[69] Spence[56] has patented a biological process for the decomposition of guayule to promote the release of rubber hydrocarbons. The decomposition of guayule resins by microorganisms for the purpose of producing improved rubber hydrocarbons has been studied by Allen et al.[3] In a similar way, bacteria and allied microorganisms may have contributed to the liberation of petroleum hydrocarbons from the organic matrix of plant and animal tissues.

Types of Bacteria Which Release Oil

From the multiple ways in which bacteria release oil from various kinds of sedimentary material, it should be apparent that many different bacterial species may contribute to the process. Particularly is this true in recently deposited sediments that are relatively rich in the organic remains of plants and animals, tissues of which may carry hydrocarbons. ZoBell[77] has listed nearly a hun-



Electron photomicrograph of a single cell of a sulfate-reducing bacterium magnified 45,000×. The arrow directs attention to the flagellum, a long, slender, whip-like appendage by which the cell propels itself through fluid medium.

dred different species of bacteria found in marine bottom deposits, where they appear to be active in the decomposition of organic matter.

An average of 160 million bacteria per gram of mud from the sea floor near Andros Island in the West Indies was reported by Drew.[21] Sediments from the Channel Island region off the coast of southern California were found by ZoBell and Anderson[83] to contain several million viable bacteria per gram (wet basis). A progressive decrease in the bacterial population in bottom deposits with depth has been noted wherever profile series were examined.[35, 44, 45, 85]

Below a depth of 10 to 20 feet, strict anaerobes predominate, and a good many of the bacteria appear to be sulphate reducers, methane producers, or other physiological types having specialized hydrogen-acceptor requirements. For example, sulfate serves as the hydrogen acceptor or as the source of oxygen for sulfate-reducing bacteria, and carbon dioxide or bicarbonate serves as the hydrogen acceptor for methane-producing bacteria:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$$

Hydrogen for sulfate-reducing, methane-producing, and similar anaerobic bacteria may come from the fermentation of organic matter,[81] the radioactivation of hydrogen-containing compounds,[50, 81] or from other reactions.[28, 38, 81]

The investigations to date indicate that sulfate-reducing bacteria are the most versatile and most widely distributed oil-releasing microorganisms. Not only can they degrade many kinds of organic matter that may contain oil but certain sulfate reducers also decompose gypsum, dissolve carbonates, produce carbon dioxide, form wetting agents, and attach themselves to the solid surfaces, thereby releasing or crowding off oil. Their versatility, together with their common occurrence in sediments and their ability to grow under a wide variety of environmental conditions, has attracted attention to sulfate reducers in studies on the bacterial release of oil.

Recent investigation indicates that methane-producing and hydrogen-liberating bacteria also contribute to the release and movement of oil in laboratory experiments. Further studies may reveal that other physiological types of bacteria are equally important.

Characteristics of Sulfate Reducers

Sulfate-reducing bacteria are single-celled microorganisms ranging in size from 0.5 to 1.0 micron in width by 1.0 to 5.5 micron in length. A micron is approximately 1/25,000 inch). They generally occur singly, although, in rapidly multiplying cultures, they may appear in pairs or short chains of cells loosely attached end to end. Young cells of all observed species are actively motile by means of one or more polar flagella. Older cells are sedentary and often appear black owing to the presence of ferrous sulfide on or in their cells.

Like other true bacteria, sulfate-reducers multiply by transverse fission, the parent cell splitting athwart the long axis into two daughter cells every hour or so. The rate of multiplication depends upon the temperature and other environmental conditions. When conditions are not favorable for their multiplication, they may remain dormant for many months, years, or possibly for centuries. Some sulfate reducers form endospores which are extremely resistant to high temperatures and other adverse conditions.

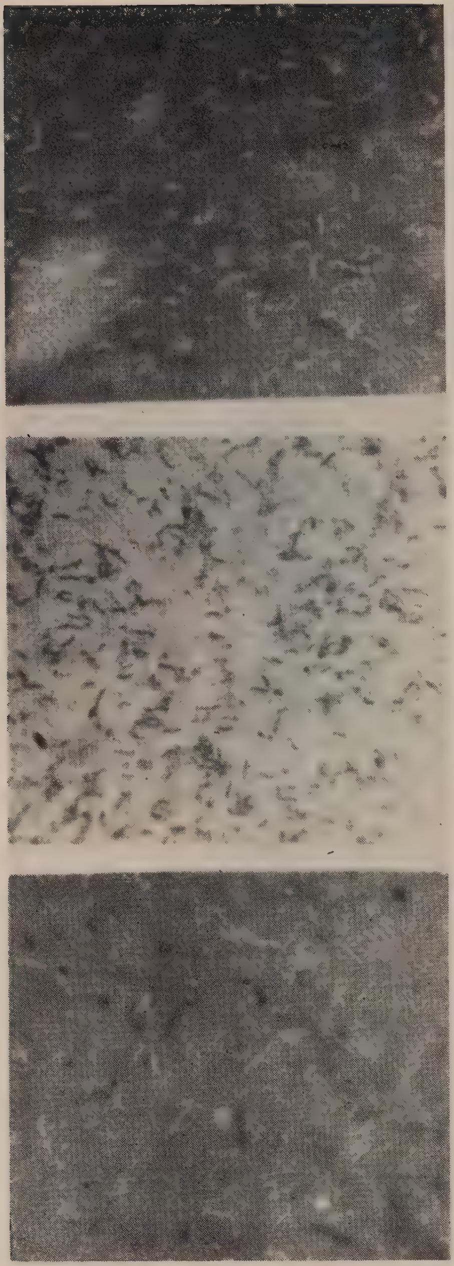
Sulfate reducers generally appear as slightly curved rods, although pleomorphic forms are common. Differences in morphology, coupled with the difficulty in obtaining absolutely pure cultures, has led to considerable confusion in naming sulfate reducers. (A pure culture is one which contains only one kind or species of bacteria as opposed to a mixed culture which contains two or more kinds of species.)

Depending upon which morphological form predominated in their cultures, early workers applied the generic terms *Bacterium, Bacillus, Spirillum, Vibrio,* etc., to sulfate reducers. The first two names are description of straight rods. *Spirillum* is properly applied only to spiral-shaped bacteria having five to twenty flagella, while *Vibrio* is the accepted generic name for curved or comma-shaped bacteria having one or more polar flagella. It is now generally agreed that *Vibrio* is the proper designation for sulfate reducers. The suffix *Desulfo* has been added to indicate curved or comma-shaped bacteria which remove sulfur, thus giving the generic name *Desulfovibrio.*

Starkey[58] has applied the name *Sporovibrio* to curved or comma-shaped sulfate reducers which form spores. Since spore formation does not appear to be a common characteristic of sulfate-reducing bacteria, *Desulfovibrio* may be a more apt generic designation.

There probably are several species of sulfate reducers, but only a few have been described. *Desulfovibrio desulfuricans* differs from *Desulfovibrio aestuarii* primarily in that the former grows best in fresh-water media and fails to develop in sea water upon initial isolation. *D. aestuarii* has the opposite characteristics, although there are other distinctive features. *D. rubentschickii* resembles *D. desulfuricans* morphologically and culturally, differing chiefly in its ability to utilize propionic, butyric, and other fatty acids. *D. thermodesulfuricans* was described as a species having an optimum temperature for growth of 55° C., but since other species can be acclimatized to grow at 55° C. or even higher, this is not a valid species distinction. Stephenson and Stickland[63] described, but did not name, a variety or species of *Desulfovibrio* (Strain 182) which differed from others in its ability to oxidize molecular hydrogen as an energy source:

$$H_2SO_4 + 4H_2 \rightarrow H_2S + 4H_2O$$



Sulfate-reducing bacteria photographed with an ordinary optical microscope (final magnification 620×).

Sulfate reducers which utilize molecular hydrogen have been observed by Starkey and Wight,[61, 73] Pont,[41] and others.[81]

ZoBell[80] named *Desulfovibrio hydrocarbonoclasticus* as a sulfate reducer which attacks petroleum hydrocarbons, the suffix *clasticus* coming from the Greek root *Klastos* meaning to break or to take apart. The prefix *halo,* a Greek combining form meaning salt, has been added to certain varieties which tolerate salt concentrations ranging from 100,000 to 300,000 parts per million. Thus *Desulfovibrio halohydrocarbonoclasticus* is a comma-shaped, sulfate-reducing organism which "breaks" hydrocarbons at relatively high salinities. Cultures of *D. hydrocarbonoclasticus,* isolated from various sources, grow readily in salt solutions ranging roughly from 5,000 to 125,000 parts per million.

The most effective oil-releasing cultures of *Desulfovibrio* were isolated from cores of limestone-sulfur-anhydrite formation taken from a depth of approximately 1530 feet from wells of the Freeport Sulfur Company at Grand Ecaille, La. Cores of the material were provided through the courtesy of G. M. Knebel of the Standard Oil Company of New Jersey. Other effective oil-releasing cultures were taken from marine muds off the coast of southern California.

Additional information and literature on the characteristics of sulfate-reducing bacteria have been catalogued by Baars,[4] Bunker,[13] Rittenberg,[46] Starkey,[58] and Tausson.[64, 66]

Propagation of Sulfate Reducers

Sulfate reducers are strict anaerobes They grow best in the absence of light Both *Desulfovibrio hydrocarbonoclasticus* and *D. halohydrocarbonoclasticus* are capable of growing in mineral salts solutions enriched with crude oil. Presumably, impurities in crude oil provide the nitrogen requirements of the bacteria. They preferentially attack certain nitrogenous and waxy constituents of crude oil, although their ability to assimilate pure hydrocarbons ranging from decane, $C_{10}H_{22}$, to dotriacontane, $C_{32}H_{66}$, has been demonstrated.[39, 64]

Cultures may be propagated in glass-stoppered bottles or other closed containers from which atmospheric oxygen can be excluded. A low redox potential,[78] E_h —0.05 to —0.35 volt, favors the multiplication of sulfate reducers. Nutrient media can be rendered reducing by the addition of 0.02 percent sodium sulfide, $Na_2S.9H_2O$, or 0.01 percent either ascorbic acid, $C_6H_8O_6$, or sodium formaldehyde sulfoxylate, $NaHSO_2.HCHO.2H_2O$.

After *Desulfovibrio* species start to grow, they create reducing conditions by producing hydrogen sulfide. Some varieties produce the equivalent of 500 to 1500 parts per million of hydrogen sulfide. Either sulfate, thiosulfate, or sulfite, seems to be essential for the growth of sulfate reducers. Sulfite is reduced more readily than sulfate.

The following medium has proved to be quite satisfactory for the growth of sulfate reducers:

Sea water	1000.0 ml.
Potassium phosphate, K_2HPO_4	0.2 gm.
Magnesium sulfate, $MgSO_4 7H_2O$	0.2 gm.
Sodium sulfate, Na_2SO_4	1.0 gm.
Sodium sulfite, Na_2SO_3	0.2 gm.
Calcium carbonate, $CaCO_3$	0.2 gm.
Ammonium chloride, NH_4Cl	0.1 gm.
Ascorbic acid, $C_6H_8O_6$	0.1 gm.
Sodium lactate, $NaC_3H_5O_3$	3.0 gm.

The reaction of the medium is adjusted to pH 7.0 to 7.5 by the addition of one-normal sodium hydroxide or hydrochloric acid as required. Sodium sulfide or sodium formaldehyde sulfoxylate may be substituted for the ascorbic acid. A variety of organic compounds or petroleum hydrocarbons can be substituted for the sodium lactate for the propagation of certain varieties of *Desulfovibrio*. All sulfate reducers do not attack hydrocarbons. For the cultivation of fresh-water strains, sea water can be diluted with distilled or tap water. For the cultivation of halophilic or salt-loving strains, sodium chloride can be added to give the desired osmotic pressure. The addition of 0.01 percent ferrous sulfate, $FeSO_4.6H_2O$, serves as a useful indicator of sulfide production.

Activity in Oil Well Brines

A good many oil-well brines tested have been found to provide all of the essentials for the growth of certain sulfate-reducing bacteria. Maliyantz,[36] observed that a variety of Russian crude oils was attacked by *Desulfovibrio aestuarii* in oil-well brines with the formation of acids and the reduction of sulfate to hydrogen sulfide. The organic acid content of the medium was increased from an initial value of 1.070 grams per liter to as high as 2.191 grams per liter. Reinfeld[43] also observed the formation of acids by sulfate-reducing bacteria in gusher oil and its accompanying water.

Further observations on the reduction of sulfates by *Desulfovibrio* species, which oxidizes petroleum hydrocarbons to organic acids, have been made by Tausson and Aleshina,[64] Tausson and Vesselov,[66] Schneegans,[48] and Novelli and ZoBell.[39]

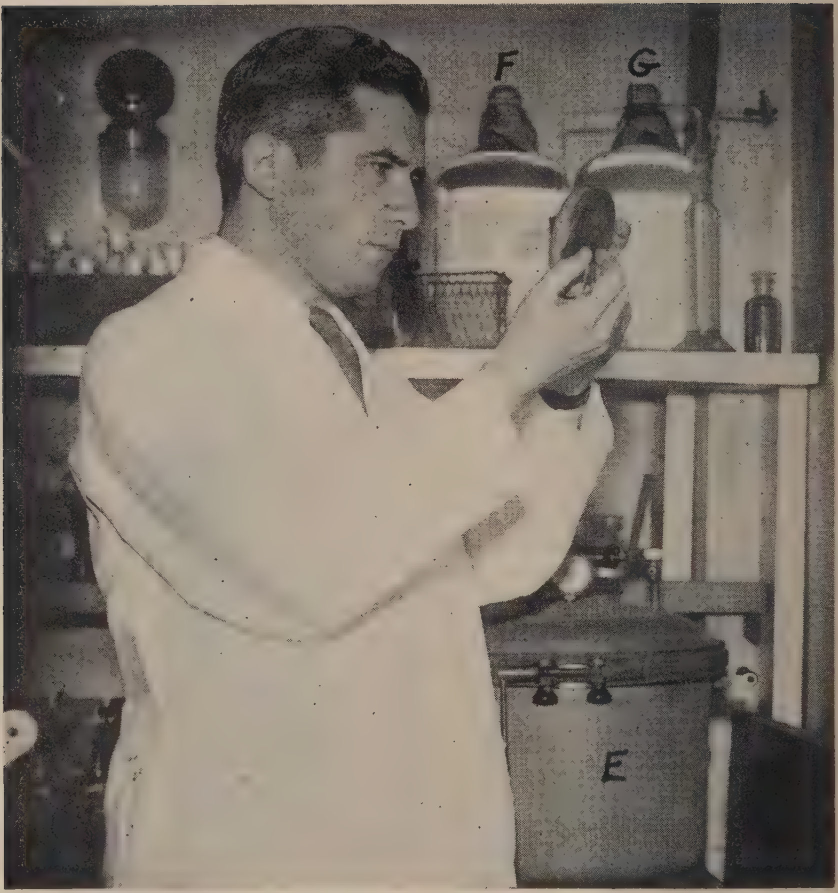
Part of the plugging action of oil-well brines being injected into Woodbine sands in the East Texas field was attributed by Morris[37] to the growth of sulfate-reducing bacteria in the brines. Alcorn[1] also reported the growth of sulfate reducers in salt-water disposal injection systems. According to Plumer and Walling,[40] the growth of sulfate-reducing bacteria in East Texas oil field waters was stimulated by the presence of ferrous sulfide.

The following amounts of germicides in 2½ liters of oil field brine were required to inhibit the growth of sulfate reducers:[40]

Phenol	2.5 gm
Lysol	2.5 ml
Monochlorobutane	3.0 ml.
Trichlorobutane	3.0 ml.
Creosote	7.5 ml.
Cresol	1.0 ml.
Formaldehyde	0.1 ml.

The occurrence of sulfate reducers in oil-well brines is well documented.[9, 10, 24, 25, 26, 31] Whether the bacteria found in reservoir fluids are species indigenous to the oil-bearing formations is problematical, because the bacteria might have been introduced at the time or after the wells were drilled, but the continued abundance of sulfate reducers in certain produced fluids proves that they grow in oil-well brines *in situ*. It may be especially significant that sulfate reducers have been found in less than one-fourth of the samples of reservoir fluids examined for their presence.

Sulfate reducers were detected in only 12 of 33 samples of produced water collected from separation tanks in the Pennsylvania Grade Crude Oil Association area. The numbers present in stored samples of the produced waters were so small as to cast doubt if any of these sulfate re-



Dr. William B. Rosenfeld, API Project 43A research associate, examining a Petri dish for the presence of bacterial colonies. At his elbow is a 24-quart pressure apparatus, E, used for the cultivation of anaerobes in an atmosphere containing no oxygen. In the bcakground are two five-gallon bottles, F and G, in which are grown large quantities of sulfate-reducing bacteria.

ducers were indigenous species, particularly since the separation tanks were subject to contamination and the bacteria present appeared to be more akin to common soil *Desulfovibrio* than to hydrocarbon-oxidizing types commonly found associated with oil. This doubt was substantiated by demonstrating the ability of strains of *D. hydrocarbonoclasticus* to grow in 28 of the 33 samples of produced waters. Dr. R. V. Hughes of the Pennsylvania Grade Crude Oil Association helped with the collection of these samples.

The recovery of sulfate-reducing bacteria from reservoir fluids coupled with their demonstrated ability to grow in such reservoir fluids and to release oil from solids by mechanisms described above suggest that such bacteria may have contributed to the migration and accumulation of petroleum in past geological ages. The rather common presence of sulfide and the relatively low sulfate content of many waters associated with oil[52] adds weight to the argument that sulfate-reducing bacteria have been active in such environments. The fact that certain *Desulfovibrio* species can grow at temperatures at least as high as 80° C. and at salinities up to 300,000 parts per million is also significant.

Methane-producing bacteria and other physiological types may likewise have contributed to the migration and accumulation of oil.

Various environmental factors and certain fortuitous circumstances probably determined whether oil-releasing bacteria were present or active in petroliferous sediments. This assumption is based upon analogy from the more thorough study of the factors which influence the distribution and activity of bacteria in soil.[70]

Although the experimental work summarized in the foregoing sections is still in the preliminary stage, and while some of the conclusions are highly speculative, the results suggest considering the introduction of appropriate bacterial cultures into oil-bearing formations for the purpose of increasing the secondary recovery of oil. Carefully selected varieties of bacteria may prove to be especially beneficial in relatively shallow wells in limestone formations where conventional acidizing is indicated. If successfully introduced, bacteria might be expected to permeate the formation in an ever-increasing sphere, producing acid, wetting-agents, and carbon dioxide and crowding oil off solid surfaces by virtue of the affinity of the bacteria for solids. The bacteria may also prove to be beneficial in the secondary recovery of oil from formations in which water flooding or water repressuring is practiced. Another possible practical application of oil-releasing bacteria is the separation of oil from tar sands, oil-saturated shales, and similar oil-bearing sediments.

The experimental work has not progressed far enough to make any definite recommendations. Much additional research work will be required to provide answers to numerous questions regarding the introduction of bacterial cultures into oil-bearing formations Those who are inclined to try the procedure are warned that only failure can be expected to result from the haphazard introduction of bacterial cultures into oil-bearing formations.

The method of introducing bacterial cultures into oil-bearing formations and the kind of culture to be introduced will depend upon the nature of the formation. The latter must be carefully diagnosed as to temperature, salinity, sulfate content, indigenous bacterial population, and other conditions that may influence the results. Cultures must be selected which are able to grow at the temperature, salinity, and hydrostatic presssure of the formation. Preliminary tests should be conducted in the laboratory to demonstrate the ability of the selected bacteria to grow in the reservoir fluid of the well or formation to be treated. Sulfate-reducing bacteria cannot be expected to grow unless sulfate is present. All bacteria require a suitable source of food and energy.

Preliminary Tests

Preliminary tests should also be conducted in the laboratory to determine whether the bacteria may have an inimical effect on the oil or the formation. Some bacteria destroy oil[55,65,67,79] and others tend to decrease the permeability of oil sands.[1,37,40] Certain types of bacteria cause the corrosion of iron and steel structures.[3,11,14,27,48,59,60,61] Obviously, harmful types of bacteria must be avoided. If preliminary analyses reveal that bacteria are already present in the formation, little or nothing may be gained by the introduction of additional organisms, although this will depend upon the types of bacteria present.

The introduction of a little nutrient material along with the bacterial cultures may promote the implantation and oil-releasing activity of the bacteria. This procedure may be most practicable where water flooding is practiced. Otherwise the added nutrients would be available to the bacteria only in a relatively small sphere. In order to be effective in the recovery of oil, the bacteria must permeate the oil-bearing formation for a considerable distance.

Desulfovibrio species appear to be admirably adapted for permeating sedimentary materials in which they grow. Sulfate-reducing bacteria are by no means dependent upon the movement of fluids for their dissipation in sediments. During their "swarm" stage the bacteria themselves are actively motile by means of flagella, and they also propel themselves by a process known as protoplasmic extrusion or extension during cell divisions. The bacteria were found to move through a water-saturated mixture of fine sand and calcium carbonate at an average rate exceeding one inch per day. Migration was equally rapid in all planes.

The author is aware of no practical application that has been made of bacterial cultures for recovering oil from oil-bearing sediments, but preliminary investigations have produced promising results.

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Much of this work has been done under the auspices of The API as a part of Research Project 43A. It is a pleasure to acknowledge the suggestions and stimulating criticisms of members of The API Advisory Committee on Fundamental Research and especially the help of G. C. Gester and G. M. Knebel in obtaining samples and otherwise expediting the work. Carl A. Young, director of the division of production of The API, also has contributed in many ways to the success of the project and was instrumental in obtaining patent protection for the public.

In accordance with the policy of The API and the University of California that all information resulting from fundamental research projects shall be made available to the public without charge, U. S. Patent No. 2,413,278, covering the bacteriological process for treatment of fluid-bearing earth formations, was assigned by the author to The API and dedicated to the public.[80]

It is not feasible for either the University, The API, or the author to provide further free information or cultures, their being neither funds nor facilities for such applied work. The author has no cultures for sale and is devoting his full time to further fundamental research work, the results of which will be reported in scientific or trade journals. Although he would like to answer every query in detail, he has been completely overwhelmed by the hundreds of requests for cultures, information, advice, etc. Oil companies or private enterprises will have to undertake any work that is done with a view to practical applications.

The Pennsylvania Grade Crude Oil Association has made important contributions to the study of the problem, some of which helped to secure patent protection for the public. The support of members of its Research Committee and especially that of Dr. R. V. Hughes, director of production research, is appreciated. This organization has been conducting a research project on the possible use of bacteria in the secondary recovery of oil with Dr. Jay V. Beck in charge. It is expected that the results of this project will be published.

Summary and Conclusions

The propagation of bacteria in nutrient media overlayering samples of Athabaska tar sand has resulted in the liberation of crude oil from the sand. Pure or partially purified cultures of sulfate-reducing bacteria slowly caused the disintegration of tar sands without perceptibly modifying or destroying any of the liberated oil.

Crude-oil was also liberated from samples of Santa Maria oily shales and other oil-saturated shales by bacterial activity. Bacteria released no oil from samples of oil shale which contained no free oil. Bacteria likewise failed to release oil from natural rock asphalt, gilsonite, or ozocerite. Traces of oil were released from certain oil-bearing sand cores.

The mechanisms by which bacteria liberate oil from solids have been investigated by experimenting with synthetic sediments saturated with oil. Certain clays and colloidal materials adsorbed oil so tenaciously that it could not be removed by treatment with either solvents or bacteria.

The decomposition of oil-saturated sulfate rocks, such as gypsum, anhydrite, or plaster of paris, by sulfate-reducing bacteria tends to liberate oil. Acids produced by bacteria help to dissolve calcium salts and particularly carbonate rocks. Adsorbed oil is released and void or pore spaces are formed, thereby providing for the migration or accumulation of oil. Hydrogen-oxidizing bacteria that reduce carbon dioxide to methane or carboxylic acids may contribute to the decomposition of carbonates.

Carbon dioxide, produced by respiring bacteria or resulting from the actions of acids or carbonates, tends to decrease the viscosity of oil. Tiny bubbles of the gas have a bouyant effect on oil droplets. Methane produced by bacteria may dissolve oil from solids or it might help to displace oil from micro-traps.

The affinity of certain bacteria for solid surfaces promotes the removal of films of oil or grease. The ability of bacteria to reduce the surface tension of nutrient media is also believed to be a factor which contributes to the liberation of oil.

Petroleum hydrocarbons bound by organic matrix in plant and animal remains might be released by the selective decomposition of organic matter.

Possibly playing a part in the separation of oil from solid sediments are many different physiological types of bacteria of which sulfate reducers appear to be the most versatile and most widely distributed in sediments. Some of the more salient properties of sulfate reducers, including their morphological and cultural characteristics, are summarized Under certain conditions the growth of sulfate reducers in oil-well brines may exert a plugging action in oil sands or they may promote the corrosion of iron or steel structures. Methane-producing and hydrogen-liberating bacteria also contribute to the release and movement of oil.

Although some of the foregoing conclusions are based upon rather fragmentary data or conjecture, it is believed that bacteria may have played an important role in the liberation, migration, and accumulation of oil throughout the geological ages. Various environmental factors and certain fortuitous circumstances probably determined whether oil-releasing bacteria were present or active.

All that can be said regarding the practical use of bacteria to increase the recovery of oil from oil-bearing formations is that it appears to be a promising field for further investigation Much more experimental and developmental work will have to be done by trained microbiologists in cooperation with petroleum engineers before any definite recommendations can be made

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Contribution No. 327

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ANTIBIOTIC PRODUCTION BY MARINE MICROORGANISMS[1]

WILLIAM D. ROSENFELD[2] AND CLAUDE E. ZoBELL

Scripps Institution of Oceanography, University of California, La Jolla, California

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The multiplication of most nonmarine bacteria is inhibited by sea water (Koinek, 1927). ZoBell (1941) found that only from 4 to 15 per cent as many baceria from soil, sewage, and other fresh-water or terrestrial sources formed colonies n nutrient agar prepared with sea water as on a similar medium prepared with istilled water. Sea water is also bactericidal for many nonmarine bacteria, ram-positive organisms being more sensitive than gram-negative forms (Beard nd Meadowcroft, 1935; ZoBell, 1936). This was demonstrated by suspending ure or mixed cultures of bacteria from various fresh-water sources in sea water r other mineral solutions and determining the percentage of survival after diferent periods of time. Although gram-negative organisms display resistance to he lethal action of sea water, their viability in this medium varies widely among ifferent species. In an investigation employing enteric bacteria, Trawinski 1929) reported survival periods in sea water ranging from 12 hours for *Shigella ysenteriae* to 23 days for *Salmonella enteritidis*. Carpenter *et al.* (1938) noted hat natural sea water killed 80 per cent of the organisms in sewage within half n hour.

The bacteriostatic and bactericidal effects of sea water are greater than can e accounted for upon a basis of its salinity or osmotic pressure. Not only is atural sea water more bactericidal than synthetic sea water (ZoBell, 1946; ZoBell and Feltham, 1933), but it is also more bactericidal than heat-treated sea water (Kiribayashi and Aida, 1933; Waksman and Hotchkiss, 1937; ZoBell, 936). De Giaxa (1889) observed that pathogens rapidly perish in raw sea water, lthough they may survive almost indefinitely in heat-treated sea water. Water rom the Black Sea was found by Krassilnikov (1938) to be germicidal for terestrial bacteria until it was boiled. He confirmed the observations of Beard and Meadowcroft (1935) and ZoBell (1936) that the bactericidal potency of sea water was decreased but not destroyed by passing it through Berkefeld, Chamberland, Coors, or similar filters.

Lacking the properties of bacteriophage, the bactericidal property of sea water s attributed primarily to its content of antibiotic substances produced by microrganisms. Credence is lent to this view by the observation that the bactericidal rinciple occurs in greatest concentration in samples of sea water recently colected from zones of maximum bacterial population. The experimental results eported below demonstrate the production of antibiotic substances by several pecies of microorganisms native to the sea.

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[2] Present address: California Research Corporation, La Habra, California.

EXPERIMENTAL RESULTS

Fifty-eight pure cultures of marine microorganisms were tested for their ant microbial activities. The cultures employed as potential antagonists were take from a collection previously described by ZoBell and Upham (1944) and we maintained in a medium of the following composition:

Difco peptone	5.0 g
Difco yeast extract	1.0 g
$(NH_4)_2SO_4$	1.0 g
$FeSO_4.(NH_4)_2SO_4.6H_2O$	0.1 g
Aged sea water (75 per cent)	1,000 ml

The solution was adjusted to pH 7.4 to 7.6 before autoclaving. When a sol medium was required, 2.0 per cent of agar was added to this solution prior t sterilization.

TABLE 1

Antimicrobial behavior of marine microorganisms

ANTAGONISTIC GENUS	SPECIES TESTED	SPECIES INHIBITING FRESH WATER OR TERRESTRIAL ORGANISMS
Bacillus	9	4
Micrococcus	6	3
Actinomyces	2	1
Serratia	1	1
Pseudomonas	19	0
Vibrio	11	0
Flavobacterium	5	0
Achromobacter	4	0
Sarcina	1	0
Totals	58	9

All fresh-water or terrestrial species were tested to ensure their growth in th sea-water medium before subjecting them to the effects of marine antagonist Both antagonistic and test inocula were taken from cultures grown for 48 hou at 27 C.

Antimicrobial effects were surveyed in pour plates, each containing 20 ml nutrient agar and seeded with 0.2 ml of a test culture. After the medium ha solidified, the marine species under investigation were streaked over quadran of the plates, which were then incubated at 27 C. Plates were examined at fr quent intervals over a period of 17 days for growth suppression of the test o ganisms, as evidenced by clearing zones adjacent to the lines of growth of marin antagonists. Table 1 outlines the results noted and summarizes the distributic of antagonistic species among the various genera investigated.

Although two antagonistic organisms were gram-negative, the majority species exhibiting inhibitory powers were members of the gram-positive gener *Bacillus* and *Micrococcus*.

The susceptibility of the test organisms is described in tables 2, 3, and 4. Of e 11 gram-positive cultures employed, only *Staphylococcus aureus* and *Strepto-*

TABLE 2

Antimicrobial spectrum of marine Bacillus species

TEST SPECIES	INHIBITED BY			
	B. borborokoites	*B. abysseus*	*B. thalassokoites*	*B. submarinus*
acillus anthracis	+	+	−	−
. megatherium	−	−	−	−
. mycoides	+	+	+	+
. subtilis	−	−	−	−
orynebacterium pseudodiphthericum	+	−	−	−
icrococcus roseus	+	+	+	+
ycobacterium lacticola	−	−	−	−
roteus vulgaris	−	−	−	−
almonella typhimurium	−	−	−	−
rcina lutea	+	+	+	+
higella paradysenteriae	−	−	−	−
aphylococcus aureus	−	−	−	−
citreus	+	+	+	+
reptococcus faecalis	−	−	−	−

TABLE 3

Antimicrobial spectrum of marine Micrococcus species

TEST SPECIES	INHIBITED BY		
	M. maripuniceus	*M. sedimenteus*	*M. infimus*
acillus anthracis	+	−	*
. megatherium	−	−	*
. mycoides	−	−	−
. subtilis	−	−	−
orynebacterium pseudodiphthericum	−	−	*
icrococcus roseus	−	−	−
ycobacterium lacticola	+	−	*
roteus vulgaris	−	−	−
almonella typhimurium	−	−	−
rcina lutea	+	+	+
higella paradysenteriae	−	−	*
aphylococcus aureus	−	−	−
citreus	+	−	*
reptococcus faecalis	−	−	*

* This species not tested.

ccus faecalis failed to undergo inhibition by one or more marine species. Three am-negative species were tested, and none of these was susceptible.

An attempt was made to demonstrate the presence of the inhibitory principle cell-free solutions prepared by filtration of the antagonistic cultures. The inhibitory organisms were grown in the broth described above for periods to 11 days, after which they were passed through Seitz or Mandler filters. reaction of all filtrates approximated pH 8 and in each case was adjusted to 7.2 before employment of the sterile solutions as inhibitory agents. Pour pla of susceptible organisms were prepared in the manner already outlined. Ste discs of filter paper were saturated with the culture filtrates and applied to agar surface. Such plates were incubated for 6 days, during which they w examined frequently for the presence of inhibition zones. The results are gi in table 5.

TABLE 4

Antimicrobial spectrum of marine microorganisms

TEST SPECIES	INHIBITED BY	
	Actinomyces marinolimosus	*Serratia marinoru*
Bacillus anthracis	−	+
B. megatherium	+	+
B. mycoides	+	−
B. subtilis	−	+
Corynebacterium pseudodiphthericum	−	−
Micrococcus roseus	+	−
Mycobacterium lacticola	−	−
Proteus vulgaris	−	−
Salmonella typhimurium	−	−
Sarcina lutea	+	−
Shigella paradysenteriae	−	−
Staphylococcus aureus	−	−
S. citreus	−	−
Streptococcus faecalis	−	−

TABLE 5

Decreases in antimicrobial activity resulting from filtration of antagonistic cultures

ANTAGONIST		SUSCEPTIBLE SPECIES	
Species	Filter	Tested	Inhibite
Actinomyces marinolimosus	Seitz	4	1
Bacillus borborokoites	Mandler	6	1
B. abysseus	Seitz	5	1
B. thalassokoites	Seitz & Mandler	4	0
B. submarinus	Seitz	4	1
Micrococcus maripuniceus	Seitz	4	0
M. sedimenteus	Mandler	1	0
Serratia marinorubra	Mandler	3	0

Little antagonistic activity was displayed by the cell-free preparations. though such results may suggest that the inhibitory substance is intimately sociated with its parent cell, there is the possibility that the active principle removed by adsorption on the filter.

DISCUSSION

Quantitative evidence of the effect of marine microorganisms upon the in-
bitory property of sea water has not been obtained. However, a presumptive
errelationship may be inferred from the incidence of antagonistic species. The
havior of antagonistic cultures when passed through germ-proof filters resem-
s that of sea water, the two undergoing similar decreases in antimicrobial
tency. Further evidence for this correlation of activity is observed in a com-
rison of data reported herein with that testing the effect of sea water upon
nmarine bacteria. Of six organisms shown by Krassilnikov (1938) to be in-
bited by unheated sea water and common to both investigations, only *Staphy-
occus aureus* failed to demonstrate a bacteriostatic response to marine bacteria.
is also significant that the response of test species to inhibition by marine or-
nisms appears to parallel the gram reaction. This is in accordance with the
neral observation that gram-positive bacteria are more often inhibited by sea
ter than are gram-negative species.

Isolations of specific antibiotics produced by marine bacteria have not been
tempted, but it is evident that various species of microorganisms indigenous
the sea elaborate antimicrobial substances. The survey reported here, al-
ough very limited in scope, suggests that the marine environment should be
nsidered as a potential source of antibiotics.

SUMMARY

Of 58 species of marine microorganisms tested, 9 have demonstrated anti-
otic activity against nonmarine forms. The most actively antagonistic marine
nera were *Bacillus* and *Micrococcus*.

Similarities in the behavior of sea water and of antagonistic marine cultures
licate that the bacteriostatic or bactericidal activity of the former may be at
st partially due to an autochthonous flora of antibiotic-producing organisms.

It is suggested that the sea may represent a reservoir of microbial antagonists
possible importance.

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Contribution No. 328

The Beach-Spawning Grunion

University of California

By BOYD W. WALKER

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The Aquarium Journal

The tale of the famous grunion—the fish that comes out of the water to spawn on the beach

THE BEACH-SPAWNING GRUNION

By Boyd W. Walker

University of California

Raised eyebrows and a you-can't-kid-me look are apt to be the first responses that a southern Californian will get when he invites a friend to go night fishing, with nothing but a sack and a flashlight for equipment. When he adds that the fish will be picked up as they flop about on the sand, his friend will probably begin talking about the traditional snipe hunt, where the gullible guest catches nothing but a cold. The southern Californian may then insist that colds aren't caught in the sunny southland, and show such obvious sincerity that his guest will agree to try the sport.

Their quarry will be the grunion, a small silvery fish that probably would be of little interest to anyone but an ichthyologist if it laid its eggs in the water as most fish do. This scaly nonconformist breaks from tradition, however, by coming completely out of the water to lay its eggs in the moist sand above the water line. As if this behavior were not strange enough, the fish make these excursions only on particular nights, and with such regularity that, with the aid of tide tables, the time when they arrive on the beach can be forecast a year in advance, usually within a fraction of an hour. From Santa Barbara, California, south into Lower California, there are many beaches where this amazing phenomenon may be seen. On certain nights, during high tide, these beaches sometimes appear as though covered by a sheet of shimmering silver, as the tho sands of wriggling fish busily depo their eggs in the sand. The spectacle exciting even when the runs are light and the fish are scattered in sm groups over the beach.

This habit of leaving the water spawn makes possible the night sp of grunion hunting. The first fish appear are announced by shouts tl can be heard up and down the bea If the run is a good one all is actio The usually quiet beach is covered w bobbing lights and laughing, screami people grabbing wildly for the slippe flopping fish. A fever seems to g the crowd, and people who at first content to stand and laugh at the tics of the others are soon behaving madly as any. No one seems immu Even the surf fishermen, who prof to disdain those who see sport in su childish behavior, are soon discardi their equipment and resorting to me ods as primitive as the others. C would think that none of the fish cou return to the ocean with so ma clutching hands to stop them; but ma do, because a small, wet, muscular f is not easy to hold in the bare hand a the use of nets or special equipment prohibited by law.

The grunion is a slender fish, with bluish back and bright silvery sides a belly. The adults average about six seven inches long, with the female u ally larger than the males. For th interested in scientific names, the t onomists have labeled it *Leurest tenuis,* and it belongs to the fam

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erinidae. The atherines, or silver-
, are primarily fishes of tropical
temperate seas. The nearest rela-
on our coast are called jack smelt
top smelts, which are misnomers,
ey are not to be confused with the
smelts of more northern waters,
h belong to the family Osmeridae
which, like trout, have an adipose
The "smelts" of California are mar-
fish and are commonly caught by
ers from piers and barges.

runion are found nowhere in the
d except on the Pacific Coast, from
terey Bay to central Lower Califor-
It is only from Ventura County
n, however, that good spawning
can be observed. The heaviest runs
California probably occur around
g Beach and San Diego, and good
have also been reported from
er California. Certain beaches ap-
better for grunion spawning than
rs, and local inhabitants can point
the locations where the best runs
r most frequently.

he grunion was discovered in 1860,
for many years attracted little at-
on. No one knew of their peculiar
ts, and they were neither rare
gh to excite collectors, nor com-
enough to be of commercial im-
nce. The first report to reach a
tific laboratory was a letter writ-
n 1914 to David Starr Jordan of
ford University. The first accounts
so cluttered with theories on the
ts of moon, tide, race suicide, and
r factors, that they were generally
issed as fishermen's yarns. It was
ntil 1919, when Will F. Thomp-
published a fine account of the
ning of the grunion,[1] that the
ing life story of these fish was clearly set forth. Subsequent research by Frances N. Clark has provided more information.[2] The delicate adjustment between the life cycle of these fish and tidal phenomena, as reported by these scientists, now attracts world-wide attention.

The grunion spends most of its life near the sandy beaches of the Pacific shore, probably not venturing far from the mainland. Like the silversides it lives close to the surface, and feeds on the small crustaceans and other animals that compose the part of ocean life known as plankton. Only during the spawning season, from February until September as extreme limits, and from March to July as usual limits, do the fish come to the beaches and make the display which poetically minded writers have called "the dance of the grunion." In early January the gonads, or reproductive organs, of these fishes start to increase in size, and by late February or early March the first batch of eggs is matured. The time of maturing is somehow mysteriously adjusted so that the eggs are ready to be spawned just at the time of a high-tide series. The female then ripens successive batches of eggs at intervals of about two weeks for the remainder of the spawning season. Spawning occurs only on the high spring tides which accompany the full moon and the new moon, and only at night.

On the night of a run, the grunion are first to be seen as they swim in with the wash of a wave, then flash back to deeper water as the wave recedes. About the time of high tide, or shortly thereafter, there is a change in behavior.

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pson. The spawning of the grunion
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Commission, Fish Bull. No. 3, 1919;
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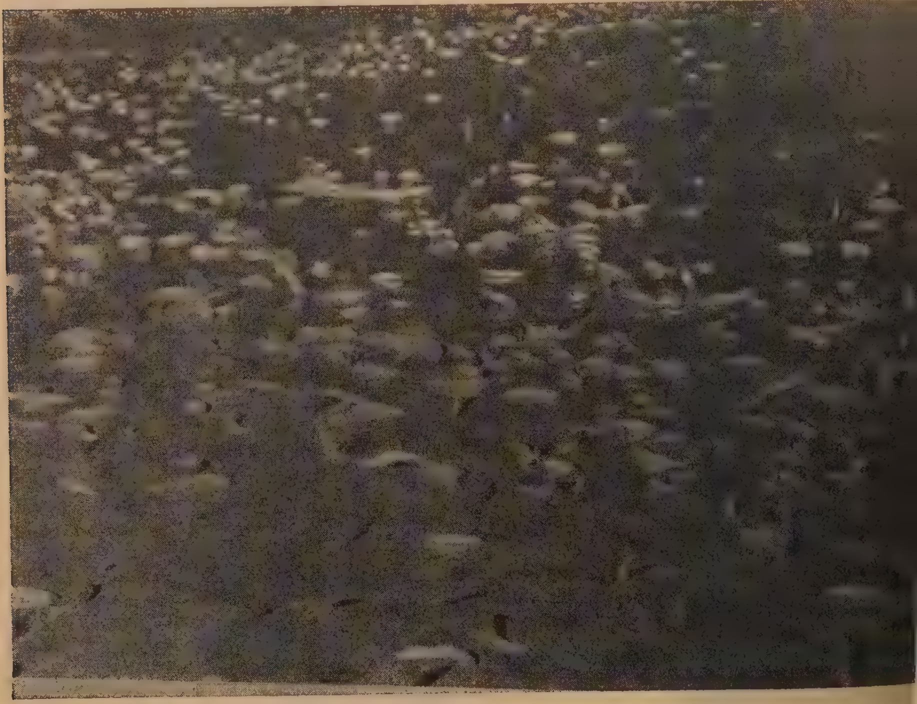
Clark, F. N. Grunion in southern California. California Fish and Game, Vol. 24, No. 1, Jan. 1938; pp. 49-54.

Then some of the fish remain on the beach after the water flows back. If watched closely it will be seen that they actually swim in with the wave and continue toward the beach as the water recedes, until they become stranded on the sand. Here they remain for a moment, and then flop back to the water or are carried out by another wave. As time passes, more and more of the fish are on the beach until, during a heavy run, they are so thick that it is impossible to walk without stepping on them. Typically the run lasts one to three hours, but the number of fish on the beach at any instant varies from none to multitudes. Finally when the tide has dropped a foot or more, the run slackens and then stops as suddenly as it started. No more fish will be seen that night, and they will not appear again until the next night, or the next run.

The entire spawning takes place while the fish are out of the water. For this reason the complete sequence
spawning behavior can be seen eas
by an interested observer.

The incoming female is accompani
by one to several males. As many
eight males have been observed matir
or attempting to mate, with one fema
If no males are present, the female w
return to the ocean with the outflowi
wave, but in their presence she swi
as far up on the sand as possible, a
digs herself in when the water reced
This is accomplished by arching t
body with the head up, and at the sar
time vigorously wiggling the tail ba
and forth. As her tail sinks into t
semifluid sand, the female twists ba
and forth, literally drilling her bo
downward until she is buried up to t
pectoral fins. Occasionally she m
bury herself completely. The male
males then curve around her, as th
lie horizontally on top of the sar
with their vents close to or touchi
her body. The female, continuing l



Grunion spawning on the beach at La Jolla, California. The fish with just their heads
showing above the sand are females depositing their eggs.

Photograph by E. C. LaFonc

isting, emits her eggs two or three hes beneath the surface of the sand. e males discharge their milt onto the nd near the female and then immetely start to wriggle towards the ter. The milt flows down about the dy of the female, and fertilization of eggs results. The spent and obvisly tired female then frees herself m the sand and returns to the sea h the next wave to reach her. The ual process of egg laying takes about seconds, but individual fish may stay the beach for several minutes. The posure appears to do them no harm, less they are stepped on by a grunion nter. Evolution has given them hardy nstitutions.

The pods of eggs thus deposited in upper tidal zone are buried deeper the sand as the beach is built up by ceeding series of lower tides. They nain in the damp sand, completely ove the wash of waves, until the next ies of high tides about two weeks er erodes the beach and washes the gs out. When the eggs are freed from sand, the baby grunion hatch out d are carried to sea. Thus there are ther delicate adjustments of the nion to tidal phenomena. The eggs en so that spawning occurs only at time of favorable tides, and after ng deposited develop rapidly so that ey are ready to hatch on the next gh-tide series. Furthermore, the eggs ll not hatch while covered by sand, t the young fish hatch out within o or three minutes after the eggs are covered. Even though the eggs are dy to hatch within nine days after ey are deposited, they still will hatch er a month or more, although the rcentage of hatching is lower. If the gs do not happen to become released the next series of high tides, two eks after they were laid, they remain dy to hatch when they are uncovered the tide one month after having en laid.

The development and hatching of grunion eggs can easily be watched in an aquarium. Fertilized eggs can be collected by digging them out of the beach where the spawning has been observed, or eggs can be stripped from live fish and artificially fertilized. Eggs which have been spawned in the sand are in clusters about 5/8 of an inch in diameter. They are salmon pink in color, and each egg is about 1/16 of an inch in diameter. Ripe fish for stripping are easily selected since a light pressure on their sides causes eggs or milt to be extruded. The best method seems to be to strip the eggs into a dry dish or saucer, and then immediately strip the milt from several males in with them, mixing eggs and milt thoroughly. After several minutes the excess milt can be washed off. Then the eggs collected by either method should be buried in sand to a depth of about three inches. If the sand is kept moist with sea water, the eggs should be ready to hatch within ten days or two weeks. When they are placed in sea water and agitated, young grunion pop out within a few minutes. Although artifiical hatching of these fish is an interesting experiment, raising the fry is difficult, and probably doomed to failure unless a continuous supply of fresh sea water is available. Even then they have never been kept alive much longer than one month.

The newly hatched fish grow rapidly during their first summer in the ocean, and continue to grow more slowly during the winter. By the following spring they are about five inches long, and many are ready for their first spawning. These young fish start spawning in April or May, but do not continue later than June. The older fish begin to spawn at two-week intervals until July, with a few stragglers continuing on into August and September. This means that almost the entire grunion population is spawning in April, May and June, but only a portion in February and March and in July, August, and September. The largest runs occur from mid-April to June.

Studies of scales show that most grunion live to be two or three years old. An occasional oldtimer attains to four years of age.

To fully understand and appreciate the striking adaptations in the timing of grunion spawning it is necessary to know something of the pattern of the tidal variations in the region where this species spawns. The major tide-producing forces are exerted by the moon and sun. Geographic conditions and other factors produce more localized variations. The heights of tides vary in cycles which tend to coincide with the fortnightly lunar cycles. During the new moon and full moon the high tides are higher than between these periods; and during the season when most of the grunion spawn, the highest tides occur at night, usually before midnight. The average interval separating the above-mentioned lunar periods is between 14 and 15 days. The highest tides of each series follow much the same cycle, the time between series showing more variation but averaging about the same. The grunion ripens a batch of eggs every 14 or 15 days, and the first batch is ripened so that they are spawned on the high-tide series just after a new or full moon. This means that the cycle of egg development in the grunion is so adjusted that spawning occurs only at these times of highest tides, and for most of the season, only on the descending tide series. In other words, on each succeeding night of the run the tides are lower than on the preceding night, thus reducing the chances for newly laid eggs to be washed out. The fact that spawning occurs at night is another advantage, for during the day gulls and other predators would take a heavy toll of fish spawning on the beach.

For the thousands of persons wh
look forward to their grunion hunt
each year, the California State Fisherie
Laboratory prepares a grunion tim
table, which gives the dates and time
when runs may be expected. Thes
tables are usually included in tide table
distributed by southern Californi
sporting goods dealers, and are ofte
published in the papers of coastal cit
ies. However, if one of these tables i
not at hand, anyone should be able t
forecast runs for himself with the in
formation given here. Figuring tha
runs start in March, there should be
run after each new moon and full moo
during that month, and each mont
thereafter through July. The runs du
ing August and September are usuall
very light, but if they do occur, th
same rules will apply. The first nigh
of the run will be either the first o
second night after the moon phase, an
the run will continue for three or fou
nights. For example, if the new moo
falls on Friday, grunion will start t
run on Saturday or Sunday, and wi
also run on Monday and Tuesda
nights.

The hour of the run can be figure
from a tide table. During March an
April it may be expected from 15 t
40 minutes before time of highest tid
after darkness, in May at about hig
tide, and during June and July from 1
to 40 minutes after the time of hig
tide. On each night grunion usual
run for one to three hours. There a
many local variations, and it must b
remembered that the fish do not vis
all beaches.

Because the grunion population w
being seriously depleted, legislation w
enacted to protect them. The fish m
be taken only with the bare hands, a
there is a closed season during Ap
and May, when it is illegal to captu
grunion by any method. In form
years nets were used, and often gre

(Continued on page 31)

each-Spawning Grunion

(Continued from page 12)

iles of fish were left on the beach by eople who had caught them just for citement. Nature cannot stand such aste, and on many beaches where forerly there were myriads of grunion ring a run, now few can be found. ith protection the grunion seem to holding their own.

Even though grunion may not be captured during April and May a trip to the beach to watch this exciting event during these months is well worth while. There is nothing to prevent watching, and the spectacle of a run of many thousands of flashing silvery fishes on a moonlit beach is certain to remain long in one's memory.

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ANAEROBIC OXIDATION OF HYDROCARBONS BY SULFATE-REDUCING BACTERIA[1]

WILLIAM D. ROSENFELD[2]

Scripps Institution of Oceanography, University of California, La Jolla, California

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Assimilation of aliphatic hydrocarbons by anaerobic bacteria has been noted n the case of *Desulfovibrio* species by Novelli and ZoBell (J. Bact., **47**, 447). The following data reveal that these sulfate reducers catalyze the anaerobic oxidation of a considerable variety of mixed hydrocarbons. Substrates were emulified in water with gum arabic, autoclaved, mixed with sterile mineral salts olution, and inoculated with mixed cultures of sulfate-reducing anaerobes. Culures were incubated in 60-ml glass-stoppered bottles at 27 C. Hydrocarbon xidation was accompanied by sulfate reduction, which was employed as an ndex of bacterial activity. Sulfates were not reduced in the presence of gum rabic mixtures containing no hydrocarbons.

SUBSTRATE	NUMBER OF CULTURES TESTED	NUMBER THAT WERE ACTIVE
rude oils:		
Calif. crude no. 138–4	27	27
Calif. crude no. 143–3	27	27
Calif. crude no. 144-1	27	26
Pa. crude no. 148–2	29	28
Pa. crude no. 148–4	29	29
efinery products:		
Kerosine no. 109–5	29	28
Lubricating oil no. 140–2	27	26
Paraffin oil	27	26
um arabic (control)	29	0

Long-chain aliphatic hydrocarbons have undergone rapid destruction by ulfate reducers. Insoluble fatty acids were isolated as intermediates in this onsumption. The presence of fatty acids, however, was transitory, for they nderwent further degradation. The utilization of hexadecane was vigorous nd was traced quantitatively by the ether extraction procedure of Gould Science, **98**, 546) and the fractionation methods of Wilson and Hansen (J. Biol. hem., **112**, 457). A typical experiment, employing culture XXIX:130-1, is corded below.

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[2] Present address: California Research Corporation, La Habra, California.

DAYS OF INCUBATION	EXTRACT FRACTIONS	
	Unsaponifiable (mg/L)	Fatty acid (mg/L)
0	910	0
13	568	120
30	48	0

Hydrocarbon utilization by *Desulfovibrio* species appears to be associated wit
the presence of a dehydrogenase system. This enzymatic activity has been de
tected by employing washed cells of pure sulfate-reducing species in the Thun
berg method. Substrates such as hexadecane or hexadecene are well suited t
the procedure and, upon activation, readily donate hydrogen to methylene blue
Nonsulfate-reducing anaerobes known to be incapable of the cultural utilizatio
of hydrocarbons were included as controls. Tubes prepared without hydroca
bon demonstrated no dehydrogenation of the gum arabic normally used t
emulsify the substrates.

SUBSTRATE	SULFATE REDUCERS		NONSULFATE REDUCERS	
	Tested	Active	Tested	Active
Hexadecane........................	3	2	4	0
Hexadecene-1......................	3	3	4	0
Gum arabic (control)................	3	0	4	0

Contribution No. 330

Reprinted from
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1947

MARINE BACTERIOLOGY[1]

By Claude E. ZoBell

Scripps Institution of Oceanography, University of California, La Jolla

The sea contains an extensive microbiological population including bacteria, yeasts, molds, diatoms, dinoflagellates, protozoa, and other microscopic organisms. By virtue of their physiological activities such microorganisms, which vary greatly in diversity of form and in relative abundance, play an important role as biochemical, geological, and hydrobiological agents in aquatic environments. Microbiology is thus a marine science co-ordinate with marine botany, chemical oceanography, marine geology, physical oceanography, and marine zoology (1). Besides being concerned with the effects of microorganisms on the biological productivity of the sea, the transformation of organic matter, and the diagenesis of marine bottom deposits, the marine microbiologist is confronted by practical problems, e.g., problems of sanitary significance, such as fish spoilage (2, 3), shellfish pollution (4), the fouling of ships' bottoms (5), and deterioration of cordage (6), rubber (7), and wooden structures (8) exposed to water. This report is concerned primarily with the biochemical activities of bacteria in the sea.

Abundance of Bacteria in the Sea

Bacteria in sea water.—Comprehensive reviews by Benecke (11) and ZoBell (12) indicate that bacteria are widely distributed in the sea, although relatively less abundant than in soil or fresh water. The numbers of bacteria found in sea water, as determined by plating procedures, range from a very few cells to hundreds of thousands of cells per ml. (13). The largest bacterial populations generally occur in water near shore where there is much terrigenous (land-born) pollution (14, 15, 16).

In the open ocean the abundance of bacteria increases from the surface downward to depths of forty or fifty meters and then decreases (17, 18) until, at depths exceeding two hundred meters, there may be fewer than one viable cell per ml. (14). The bacterial population is not detectably restricted by the high hydrostatic pressure (12), the low temperatures (19) characteristic of the deep sea, nor by solar radiation (20) in surface waters. The paucity of organic matter seems to be the principal factor which limits the bacterial population, a condition which is indicative of the efficiency of bacteria in destroying organic matter in the sea.

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 330.

Effect of phytoplankton.—The abundance of bacteria in sea water appears to be more closely related to the abundance of phytoplankton than to any other ecological factor. Gran (21) observed that the bacteria varied with the diatom content in the Gulf of Maine. A similar parallelism between bacteria and plankton was noted by Waksman *et al.* (22) in sea water, and by Henrici (23) in Lake Alexander.

According to Pütter (24), heterotrophic bacteria in the euphotic zone get much of their food from organic substances secreted by phytoplankton. Although there is some evidence (25, 26, 27) for secretion of organic substances by phytoplankton, their significance in the nutrition of bacteria has been questioned (28, 29, 30). Waksman *et al.* (31) found no evidence that living diatoms nourish saprophytic bacteria, although large bacterial populations were found associated with dead diatoms undergoing decomposition.

Effect of solid surfaces.—Bacteria occur only to a very limited extent floating free in the water, most of them being attached to plankton organisms. ZoBell (32) has attributed this to the beneficial effects of solid surfaces which tend to concentrate organic nutrients, retard the diffusion of bacterial enzymes, and provide a resting place for sessile bacteria. The beneficial effects of solid surfaces for bacteria in dilute nutrient solutions have been amply confirmed (33 to 36).

The sessile habit of aquatic bacteria is the basis of the submerged slide technic employed by Henrici (37, 38) and others (39, 40, 41). Kusnetzowa (42) and ZoBell (32) have reported that there are many aquatic bacteria which grow only when attached to solid surfaces. Indirect evidence for the adsorption of organic matter by solid surfaces in sea water has been presented by Harvey (43). Most of the bacteria in marine bottom deposits appear to be adsorbed on or attached to particles of sediment (44).

Bacteria in bottom deposits.—It is in bottom deposits where bacteria are most abundant in the sea. Drew (45) found an average of 160,000,000 bacteria per gram of mud from the sea floor near Andros Island in the West Indies as compared with a maximum count of 160 per ml. in the overlying water. Lloyd (46) found

300,000 bacteria per gram of dry mud from the Clyde Sea. Bavendamm (47) detected up to 16,800,000 bacteria per gram (wet weight) of calcareous mud from around the Bahama Islands. Bacterial populations ranging from a few thousand to 500,000,000 per gram have been demonstrated in bottom deposits from inland lakes and seas (48, 49, 50). Mare (51) estimated from plate counts that mud contained from 0.3 to 2 mg. of living bacteria per gram (dry basis).

Wherever profile series have been examined, a progressive decrease in the bacterial population of bottom deposits from the surface downward has been observed (15, 46, 48, 52, 53, 54). Waksman *et al.* (22) found bacteria at the bottom of mud cores 90 cm. long, and Rittenberg (55) detected appreciable numbers at the bottom of mud cores exceeding 350 cm. in length.

Types of bacteria in marine muds.—At the mud-water interface aerobes predominate, although most of the bacteria are facultative in their oxygen requirements. With increasing depth of mud, bacteria capable of growing aerobically decrease in abundance more rapidly than those which grow in the absence of free oxygen, and at depths exceeding 10 to 20 cm. anaerobes generally predominate (56). Collectively, the mud microflora is physiologically very versatile, being able to catalyse the transformation of a large variety of organic and inorganic compounds (11, 12, 22, 47, 52, 56 to 59).

Characteristics of Marine Bacteria

Morphology.—The predominant bacteria which Lloyd (46) isolated from Clyde Sea mud were small, gram-negative, asporogenous rods. However, Butkevich (60), who demonstrated from a hundred to a thousand times more bacteria in Barents Sea mud by direct microscopic counts than by plating procedures, concluded that most bacteria in bottom deposits are spore formers. While spore formers (species of the genera Bacillus and Clostridium) may predominate in mud from great depths, the majority of marine bacteria (both species and total numbers) appear to be asporogenous (12). About 80 per cent of the marine bacteria catalogued by ZoBell & Upham (61) are gram-negative rods, and about the same percentage was found to be actively motile by means of flagella. Predominating in the order named were species of Pseudomonas, Vibrio, Flavobacterium, Achromobacter, and Bacterium (12). One or more species of sixty other genera have been found in the sea.

The preponderance of species of Pseudomonas and Vibrio in the sea may be contrasted with the preponderance of species of Bacillus and Actinomyces ordinarily found in soil. There seems therefore to be a characteristic marine bacterial flora (13). Although there are no infallible criteria for the differentiation of marine from nonmarine bacteria, most of the bacteria found in the sea at places remote from possibilities of terrigenous contamination are unlike bacteria from other environments (12, 13, 61).

Pigmentation and photogenesis.—Typical of water bacteria, nearly 70 per cent of the bacteria from the sea are chromogenic under favorable conditions (16). Pigmentation is somewhat more common in marine bacteria than in those from fresh-water lakes (62) and far more common than in soil bacteria. Bioluminescence is also preponderantly a property of marine organisms (63), although only a small percentage of the bacteria found in the sea are photogenic. ZoBell (12) has compiled a list of thirty-four species of photogenic bacteria which have been isolated from the sea by various workers.

Cultural requirements.—Most marine bacteria require either sea water or isotonic mineral solutions for their growth (64, 65, 66). While there are some euryhaline varieties, the majority of bacteria recently isolated from the sea will not tolerate solutions more hypotonic than twelve atmospheres or more hypertonic than thirty-six atmospheres (12). The osmotic pressure of sea water of average salinity, 3.5 per cent, approximates twenty-four atmospheres. Although marine bacteria are often characterized as halophilic, it is noteworthy that most species are just as sensitive to increased salinity as to hypotonicity. This may be illustrated by the following comparative counts obtained by plating bacteria from various habitats on nutrient media prepared with balanced mineral solutions of different salinities:

	Salinity of nutrient media					
Source of bacteria	30%	15%	7.0%	3.5%	2.0%	0.5%
	average growth index					
Sea water	0.0	7.4	38.3	100.0	61.7	19.2
Marine mud	0.2	6.1	43.5	100.0	54.2	23.9
Great Salt Lake	100.0	72.2	26.3	14.1	8.0	1.7
Marine saltern	100.0	64.9	30.4	19.6	12.6	4.3
Garden soil	0.4	4.6	9.8	25.2	56.1	100.0
Sewage	0.0	2.7	5.7	13.5	44.8	100.0

It is apparent from these data that while marine bacteria are halophilic relative to sewage or soil microflora, they are not nearly so halophilic as bacteria found in marine saltern brines or Great Salt Lake (67). The Russian limans (68), the Dead Sea (69), and other strong brines (70) contain helophiles which grow readily in solutions containing from 20 to 30 per cent sodium chloride, and many of these bacteria actually require 10 to 15 per cent salt for their growth.

Temperature requirements.—Since the temperature range of the ocean bottom varies, for the greater part, from 2° to 20°C., it is not surprising that most marine bacteria grow best at relatively low temperatures. Unlike soil or fresh-water microflora, very few marine bacteria grow at temperatures as high as 30°C., and 37°C. may be lethal (71). Although their optimum is generally in the neighborhood of 12° to 25°C., most species of marine bacteria (71, 72) multiply slowly and are otherwise physiologically active at 0° to 4°C. Many species (73 to 76) are physiologically active at −3° to −7.5°C.

ACTION OF MARINE BACTERIA ON ORGANIC MATTER

Organic content of sea water.—Organic matter is quite evenly distributed throughout the sea, the content being uniformly small except in the vicinity of land or bottom deposits. An average of 4.2 p.p.m. was found in the open ocean by Krogh (30), who reported further (77) that the ratio of dissolved to particulate organic matter is about 300 to 1. The low concentration of organic matter explains why the sea has been called the world's largest and most efficient septic tank; considerable organic matter enters the sea with terrigenous drainage and more is produced in the sea by photosynthetic organisms but it is quite effectively destroyed.

Much of the dissolved organic matter in sea water is quite refractory, although it gradually undergoes bacterial decomposition when incubated under favorable conditions. Keys, Christensen & Krogh (78) estimated that only 10 to 14 per cent of the dissolved organic matter in sea water was consumed by bacteria, but Waksman & Carey (79) found that from 25 to 50 per cent was decomposed within ten or twelve days at 22°C. ZoBell & Grant (34) reported that after six months' storage in the dark the organic content of sea water was reduced from an initial 4.2 p.p.m. to 0.2 p.p.m. According to Waksman & Renn (80), about 60 per cent of the organic matter decomposed is completely oxidized and about 40 per cent is converted into bacterial cell substance. The rate of decomposition was faster at 22°C. than at higher or lower temperatures, but after prolonged incubation, as much organic matter was decomposed at 4°C. as at 22°C.

The bacterial oxidation of organic matter in sea water was found by ZoBell (81) to be independent of the partial pressure of oxygen between 0.31 and 12.74 ml. per liter. The proximity to solid surfaces appears to be one of the principal factors which influences the rate at which organic matter in sea water is decomposed (32).

Decomposition of marine plankton.—The bacterial decomposition of plankton organisms in sea water is accompanied by oxygen utilization (58, 79, 80), ammonia production, carbon dioxide formation, and phosphate liberation (81, 82). In an experiment conducted by Waksman, Carey & Reuszer (83), about one half of the nitrogen in zooplankton was liberated as ammonia and about one fifth of the carbon as carbon dioxide in nineteen days at 16° to 20°C. In another experiment (84) it was found that the amounts of ammonia produced and phosphate liberated were proportionate to the number of copepods added to sea water.

The bacterial decomposition of mixed net plankton suspended in ten to fifteen liters of sea water and stored in the dark at 20° to 25°C. was observed by von Brand and associates (85). A decrease in the plankton count was accompanied by ammonia production which reached a maximum after fourteen to twenty-five days and then decreased as nitrites and, later, nitrates were produced. Under anaerobic conditions the initial stages of decomposition took place more slowly than under aerobic conditions, and no nitrite or nitrate was developed (86). The nature of the particulate organic matter (87) was of greater importance than the concentration in determining the rate of decomposition. With recurrent supply of plankton, the formation of ammonia, nitrite, and nitrate took place simultaneously (87). Plankton organisms were decomposed at temperatures as low as 1° to 2°C., but the rate of decomposition was more than doubled by an increase of 6° or 8° in temperature (88). Johnson (89) reported the average Q_{10} for marine bacteria to be 2.3 between 5° and 15° and 2.18 between 15° and 25°C. He found that resting bacteria consumed oxygen in sea water at the rate of 2.8 to 185×10^{-12} mg. per cell per hour at 25°C.

Decomposition of carbohydrates.—Although, as a class, marine bacteria are somewhat less saccharolytic than either soil or freshwater microflora, virtually all kinds of carbohydrates ranging from simple sugars to complex polysaccharides are attacked by certain marine microorganisms (61). The addition of 4 mg. of glucose per liter of sea water was found by Waksman & Carey (90) to increase bacterial oxygen consumption about threefold, but the glucose was quantitatively oxidized only upon the addition of available nitrogen. Waksman & Renn (80) observed that the rate of glucose oxidation in sea water was directly proportional to the concentration of available nitrogen.

Several species of marine fungi studied by Barghoorn & Linder (91) utilized xylose, galactose, maltose, starch, cellulose, or pectin. Using the minimum dilution method, ZoBell (56) demonstrated 10,000 starch hydrolyzers per gram of marine mud, as compared with 100,000 glucose fermenters and 1000 cellulose digesters. Cellulose-decomposing bacteria were found by Waksman *et al.* (83) to be generally present in sea water and more abundant in bottom deposits and diatom tows. Most of the cellulose decomposers were aerobic, but anaerobic forms were demonstrated. A variety of sugars were utilized by the cellulose decomposers. Bavendamm (47) found aerobic cellulose digesters in all marine mud samples, and anaerobic cellulose digesters in many samples which he examined. Stanier (92) isolated and described four new species of bacteria which digest agar as well as cellulose.

Agar digestion.—ZoBell (12) estimated that between 1 and 2 per cent of the colonies which developed on nutrient agar inoculated with sea water or marine mud were agar digesters. Lundestad (93) described seven new species of agar digesters occurring along the coast of Norway. Waksman & Bavendamm (94) demonstrated from 50,000 to 200,000 agar digesters per gram of mud from the Bahama Island region. A new species was isolated which liberated much of the carbon from agar as carbon dioxide. Part of the carbon was utilized for the synthesis of bacterial cell substance. Under unfavorable conditions for growth, the organisms liquefied agar with the accumulation of reducing sugars.

Angst (95) named as new species, thirteen agar digesters from Puget Sound, but unfortunately described them inadequately. Two of the three new species of alginic acid-oxidizing bacteria described by Waksman, Carey & Allen (96) were able to digest agar. Seven species of agar digesters, including five new ones, were described by Stanier (92). Among the sixty new species of marine bacteria described by ZoBell & Upham (61) seven were agar digesters.

Humm (97) has carefully described all known marine agar digesters, including seventeen new species from the coast of North Carolina, where from 2 to 150 agar digesters were demonstrated per ml. of sea water and from 80,000 to 20,000,000 per gram of mud. All of Humm's agar digesters utilized glucose, fructose, galactose, mannose, cellobiose, and maltose; 90 per cent utilized xylose and lactose; 85 per cent utilized sucrose and salicin; and 53 per cent utilized arabinose, raffinose, and glycerin.

From 10 to 15 per cent of the agar digesters utilized sugars without producing acid and virtually none of them produced gas (97). ZoBell (12) has pointed out that it is a rather common property of marine bacteria to utilize carbohydrates without the production of either acid or gas. This may be attributable to the ease with which organic acids, usually produced during the dissimilation of sugars, are oxidized by marine bacteria. Nearly all of Humm's agar digesters utilized succinic acid, 70 per cent utilized lactic acid, and 65 per cent utilized acetic acid (97). Propionic, citric, malic, gluconic, maleic, malonic, mucic, tartaric, valeric, and butyric acid were also utilized by some cultures. About 70 per cent of the agar digesters attacked alginic acid, 20 per cent attacked cellulose, and 25 per cent attacked chitin.

Chitin decomposition.—Carbon dioxide and ammonia production resulted from the decomposition of chitin by marine bacteria studied by ZoBell & Rittenberg (98). Acetic acid and reducing sugars were detected in some cultures. Certain chitinoclastic bacteria utilized purified chitin as a sole source of carbon and nitrogen, whereas others attacked chitin only in the presence of supplementary carbon or nitrogen compounds. Chitinoclastic bacteria appear to be widely distributed in marine bottom deposits (22, 33, 56, 97, 99). Such bacteria have also been found by Hess (100) in large numbers associated with lobsters having a shell disease and on decomposing crabs by Hock (99) and Johnson (101).

After finding chitinoclastic bacteria in eight out of twenty-seven samples of marine salt, Stuart (102) expressed the view that such bacteria may be responsible for damage to skins and hides cured with salt.

Proteins and other nitrogenous compounds.—As a class, marine bacteria are actively proteolytic, rapidly decomposing most nitrogenous compounds with the liberation of ammonia and carbon dioxide. All of the sixty pure cultures studied by ZoBell & Upham (61) liberated ammonia from peptone, forty-seven of them liquefied gelatin, and thirty hydrolyzed casein. Proteolytic organisms predominated in the 530 samples of mud examined by Düggeli (50). Hecht (103) found that proteins were much more susceptible to bacterial decomposition than other components of the bodies of invertebrates, birds, and mammals which he buried in mud. Marine fish are extremely susceptible to bacterial decomposition as manifested by the rapid production of ammonia, indole, trimethylamine, histamine, hydrogen sulfide, and other protein-decomposition products (104 to 107). Plankton organisms, particularly zooplankton rich in proteinaceous material, undergo rapid decomposition in sea water (83, 84).

Asparagine, aspartic acid, glutamic acid, alanine, propionamide, acetamide, sodium hippurate, urea, and creatinine were utilized as a sole source of either nitrogen or carbon by most of the fifteen representative aerobic bacteria of marine origin studied by Ostroff & Henry (108). Cystine, betaine, pyridine, and uric acid were utilized by some of the bacteria. Only one culture utilized tyrosine. Neither guanidine, aniline, nor ethylamine was utilized by any of the organisms (108). From 2 to 4 mg. of glycine, alanine, phenylalanine, glutamic acid, tryosine, and asparagine per liter of sea water were found by Waksman & Renn (80) to be almost quantitatively decomposed by bacteria in two to five days at 20°C. All of the agar digesters studied by Humm (97) could obtain their nitrogen requirements from *l*-leucine, and 94 per cent from either glutamic acid, *d*-arginine, or aspartic acid.

Ammonia is generally liberated from organic nitrogen compounds whenever the nitrogen content exceeds the requirements of the attacking bacteria. Urea is readily ammonified by urea-fermenters, which appear to be quite abundant in the sea (47, 56, 109, 110). Rubentschik (111) found urea-decomposing bacteria in all samples taken from Russian limans. Ammonia was liberated from urea at temperatures as low as −2.5°C.

BACTERIAL TRANSFORMATION OF INORGANIC NITROGEN

Ammonia utilization.—Besides the ammonia liberated by the microbial decomposition of nitrogenous compounds, much ammonia is excreted by marine animals along with urea, uric acid, etc. Urea is partly dissociated into ammonium and cyanate ions. According to Cooper (112), the equilibrium constant indicates that in sea water urea is mostly dissociated. Appreciable quantities of ammonia also enter the sea in river water and rain (58). Ammonia is assimilated directly and in preference to other forms of nitrogen by many plants (113), including marine phytoplankton (112 to 117). The photochemical oxidation of ammonia in sea water to nitrite and nitrate by sunlight has been demonstrated by ZoBell (118) and confirmed by Rakestraw & Hollaender (119), but owing to the opacity of sea water to ultraviolet radiations, this process is believed to be of no importance below a depth of one meter.

There are no valid estimates on what proportion of the ammonia in the sea is utilized directly by plants as compared with the amount that is oxidized by bacteria to nitrite and subsequently to nitrate. However, data compiled by Rakestraw (120) on the distribution of nitrogen compounds in the sea indicate that relatively large quantities of ammonia must be oxidized by bacteria, particularly below the photosynthetic zone. Nevertheless, conventional enrichment culture procedures generally fail to demonstrate the presence of nitrifying bacteria in sea water except near land (11, 12, 112). Waksman *et al.* (121) concluded that there are few or no nitrifying bacteria in sea water beyond the zone of terrigenous drainage, although active nitrifiers were found in bottom deposits. Similar observations were made by Issatchenko (122) and also by Carey (123), who has reviewed the literature on the subject. The oxidation of ammonia liberated from decomposing plankton in sea water was observed by von Brand *et al.* (85 to 88). Nitrification was inhibited by low temperatures characteristic of deep sea bottoms (124).

The activity of pure cultures of nitrifiers isolated from bottom deposits (125) was found to be favored by redox potential values typical of aerated sea water, but conditions are much too reducing in most marine muds (126) to permit nitrification. Cooper (112), who has marshalled convincing evidence in favor of the intermediate formation of hyponitrite during the bacterial oxidation of ammonia to nitrite, concluded from his studies that immediately above the sea bottom, nitrification is of great importance.

Oxidation of nitrite to nitrate.—Most attempts to demonstrate bacteria in the sea which oxidize nitrite to nitrate have yielded negative results, although such organisms have been found in marine bottom deposits (121, 123), and there is ample evidence that such organisms are functional in sea water (86, 120). The oxidation of nitrite to nitrate is inhibited less by low temperatures, 1° to 2°C., than is the oxidation of ammonia to nitrite (124).

Nitrate reduction and denitrification.—Dating from 1899 when Brandt (127) advanced his hypothesis that the bacterial destruction of nitrate limited the growth of phytoplankton in tropical seas, numerous workers [see reviews by Benecke (11) and Waksman *et al.* (121)] have demonstrated a great variety of bacteria in the sea which are capable of reducing nitrate and nitrite in nutrient media, but the extent to which conditions in the sea are conducive to such activities is problematical. According to Waksman *et al.* (121), the activities of denitrifiers are so limited under marine conditions as to render them of little importance in limiting the nitrate content of sea water.

Rakestraw (128) expressed the belief that the bacterial reduction of nitrate may on occasion account for nitrite found in the sea at depths ranging from 25 to 150 meters. Braarud & Klem (129) observed the reduction of nitrate in sea water stored in the dark. The addition of 0.2 mg. of ammonium per liter of sea water retarded nitrate reduction, but it was not stopped by the addition of half this quantity of mercuric chloride. Similar observations were made by Kreps (130), who, after observing nitrate depletion in samples which had been passed through a Seitz filter, credited bacterial enzymes in sea water with the ability to reduce nitrate. Cooper (112) concluded that bacterial denitrification in aerated sea water containing adequate organic matter for energy is thermodynamically possible, but even so, nitrate reduction cannot account for all cases of nitrite occurrence in mid-water.

Drew (131) credited marine denitrifiers with the ability to promote the precipitation of calcium carbonate in tropical seas, a problem which has been extensively studied (47). Accumulating evidence [see reviews by ZoBell (12) and Bavendamm (47)] indicates, however, that except in highly localized environments there is insufficient organic matter in the sea to provide for the activities of denitrifiers.

Nitrogen fixation.—The occurrence in the sea of an abundant population of nitrogen-fixing Azotobacter and Clostridium species has been reported (11, 47, 121), but the extent to which nitrogen fixation actually takes place in the sea is yet to be determined. The salinity requirements of the Azotobacter and Clostridium species found associated with marine algae by Issatchenko (122, 132) led him to believe that these nitrogen fixers were specifically adapted to sea water. Korinek (133) found bacteria in the sea resembling Azotobacter morphologically, but he failed to find any which would fix nitrogen. Except for the sporadic presence of nitrogen-fixing bacteria, there is no evidence of nitrogen fixation in the sea, according to von Brand *et al.* (124).

REGENERATION OF PHOSPHATE

The rapid liberation of phosphate from marine plankton undergoing bacterial decomposition has been observed (31, 82, 84, 134). Phosphate was liberated from decomposing zooplankton somewhat more rapidly than from phytoplankton (134). Phosphate was not liberated from bacteria-free diatoms undergoing autolysis, but was rapidly liberated from dead bacterial cells [Renn (135)].

Hydrographic data indicated to Seiwell & Seiwell (134) that most organic decomposition and hence phosphate regeneration takes place above the oxygen minimum layer, roughly 600 to 800 meters. This is in agreement with the observations of Rakestraw (120) and Redfield (136) on the distribution of phosphate in the Atlantic. Herbivorous zooplankton feeding on diatoms were found by Gardiner (137) to excrete considerable quantities of phosphate.

MICROBIAL TRANSFORMATION OF SULFUR COMPOUNDS

Hydrogen sulfide production.—In bottom deposits from the Clyde Sea, Ellis (138) found from 10,000 to 3,000,000 saprophytic bacteria per gram, nine tenths of which could liberate hydrogen sulfide from albuminous material. ZoBell (56) demonstrated from 10,000 to 1,000,000 such bacteria per gram of mud from the Pacific Ocean. Under anaerobic conditions, organic sulfur is converted almost quantitatively into hydrogen sulfide by mixed cultures of bacteria occurring in marine mud. Aerobes also liberate hydrogen sulfide from organic compounds, but the sulfide may be spontaneously oxidized as fast as it is liberated in oxygenated sea water.

In stagnant water, hydrogen sulfide may accumulate in concentrations sufficiently high to be lethal for the flora and fauna. Such conditions have been observed in the Black Sea (139, 140, 141), the Caspian Sea (49), Odessa limans (140, 143), Lake Ritom

(144), Norwegian fjords (145), brackish water (146), parts of the Atlantic Ocean (147), and in other bodies of water having poor vertical circulation. The hydrogen sulfide has been shown to result from the bacterial decomposition of organic matter and, more important, from the reduction of sulfate.

Sulfate reduction.—The occurrence of sulfate-reducing bacteria in marine environments has been recorded by several investigators (47, 56, 109, 147 to 150). Rittenberg (151) found such bacteria in numerous mud samples from the Pacific Ocean, but only rarely were sulfate reducers detected in sea water from the open ocean. A decrease in the sulfate content of mud with increasing core depth is indicative of the activity of sulfate reducers *in situ*. The low concentration of sulfate in many oil field waters together with the presence of sulfide (152, 153) is also suggestive of the action of sulfate reducers in ancient marine sediments. The reported presence of sulfate-reducing bacteria in oil-well brines (154, 155, 156) would be more significant if shown to be indigenous species and not merely adventitious organisms introduced by drilling or pumping operations. The demonstrated ability of sulfate reducers to modify hydrocarbons (148, 157 to 160) is noteworthy, although the part played by bacteria in the formation and transformation of petroleum is still indeterminate.

From North Sea coast water, van Delden (161) isolated a sulfate reducer, now known as Desulfovibrio aestuarii, which differed from other varieties primarily in that it required sea water or 3 per cent sodium chloride for its growth. Baars (162), however, claimed to have acclimatized the marine organism to grow in fresh-water medium, an observation which Rittenberg (151) was unable to repeat with sulfate reducers isolated from the sea. According to Rittenberg (151), the maximum rate of hydrogen sulfide production in 3 per cent salt medium was about 8.4×10^{-11} mg. per cell per hour at 30°C. The Q_{10} for sulfate reduction in 3 per cent salt medium was 2.3 between 20° and 30°C. The marine sulfate reducer used neither nitrate, phosphate, selenate, tellurate, sulfonate, sulfone, nor sulfoxide as hydrogen acceptor.

Sulfur bacteria.—At least twenty species representing seven genera of achromic sulfur bacteria, which oxidize sulfide, elementary sulfur, thiosulfate, or tetrathionate, have been found in the sea (12). Some of these appear to be exclusively marine species (138, 143), while others live in both marine and nonmarine habitats

(47, 138, 163, 164). Achromic sulfur bacteria, along with purple forms (138, 163, 164, 165), are abundant in shallow water where hydrogen sulfide is being produced. Whether the hydrogen sulfide is oxidized to free sulfur or to sulfate depends upon the bacterial species, oxygen tension, concentration of hydrogen sulfide, light penetration, and other factors (166, 167).

In localized regions, purple bacteria sometimes occur in sufficient abundance to impart a red or "bloody" coloration to the water (138, 165, 168). They are independent of salinity throughout the range of 0.05 to 7.5 per cent sodium chloride, according to Baas Becking (164), who states further that they prefer diffuse or subdued sunlight, a low oxygen tension, and hydrogen sulfide, which is provided largely by sulfate reducers. Further information on the physiology of this group of bacteria is given in treatises by van Niel (166, 167, 169) and Gietzen (165), the latter dealing specifically with marine Thiorhodaceae.

Activities of Marine Microorganisms as Geological Agents

Calcium carbonate precipitation.—Several investigators (45, 47, 131, 170, 171, 172) have demonstrated the ability of certain bacteria to promote the precipitation of calcium carbonate in sea water enriched with nutrients. Lipman (173, 174) questioned the ability of bacteria to precipitate calcium carbonate from sea water to which no nutrients were added, a conclusion which was based upon the paucity of bacteria found in the open ocean. However, this objection has been nullified by the observed abundance of bacteria in calcareous bottom deposits (47).

Either denitrification (45, 131), sulfate reduction (170), ammonia production (172), oxidation of organic acids (175), or other microbiological processes which increase the pH may promote the precipitation of calcium carbonate. The reverse processes, which take place in certain parts of the ocean, tend to dissolve calcareous deposits (12, 47). Bavendamm (47), who has summarized the literature on the subject, concluded that calcium precipitation in tropical seas is primarily a microbiological process, but that there are no specific "calcium bacteria" endowed with this ability. Such processes take place only in localized sections of the ocean. In his review of the literature, Baier (175) claimed that microorganisms may influence calcium carbonate equilibrium by their effects on the pH, by producing or consuming carbon dioxide, by oxidizing organic calcium salts, or by assimilating calcium.

Deposition of iron and manganese.—There are several ways in which bacteria are instrumental in the deposition and transformation of iron and manganese (176, 177, 178). The development of iron bacteria in saline chalybeate waters has been demonstrated by Cholodny (179). Thiel (180) reported the occurrence of numerous heterotrophic bacteria which precipitated iron and manganese in marine muds. Species of iron-depositing Gallionella were isolated from the Petschora Sea and White Sea by Butkevich (181). Bacteria were believed by Issatchenko (182) to be the chief agents in the formation of pyrite.

Effects of bacteria on pH and E_h of sediments.—Bacteria appear to be the principal dynamic agencies which influence the hydrogen ion concentration and oxidation-reduction potential of bottom deposits (126, 183), by catalyzing the transformation of both organic and inorganic constituents of mud. In the presence of organic matter, bacteria create reducing conditions by consuming oxygen and producing hydrogen sulfide and other reducing agents. The oxidation-reduction potential as well as the hydrogen ion concentration is believed to have a pronounced effect on the composition, chemical reactivity, diagenesis, color, biological population, and other properties of recent sediments (126).

The ability of bacteria to consume oxygen in bottom deposits (53, 81, 184, 185) more rapidly than it can be replaced by diffusion, oceanic circulation, or photosynthetic processes promotes reducing conditions. In a reducing environment aquatic bacteria tend to attack organic matter with the formation of organic complexes, methane, hydrogen, hydrogen sulfide, carbon dioxide, ammonia, and phosphate, whereas under aerobic or oxidizing conditions the last three named products together with sulfate predominate. Reducing conditions in marine sediments are believed to favor the conversion of organic matter into petroleum hydrocarbons (186).

Role played by bacteria in petroleum formation.—By splitting nitrogen, sulfur, phosphorus, and oxygen from organic matter, marine anaerobes tend to increase the percentage composition of hydrogen and carbon, thereby producing substances which are more petroleum-like than the original organic matter (187). Methane was the only hydrocarbon observed by Thayer (188) to result from the anaerobic fermentation of either diatoms or fatty acids mixed in marine muds, but a liquid oil resembling balkhashite was obtained by Sturm & Orlova (189) from the action of anaerobes on palmitic acid and other lipids. According to Stadnikow (190), lipolytic anaerobes growing on fat-rich algae produced unsaponifiable compounds, including some petroleum hydrocarbons. A slight increase in the unsaponifiable content of decomposing algal lipids was observed by Rosenfeld (191). In similar experiments reported by Clarke & Mazur (192), diatoms stored with mud showed a decrease in the amount of free fatty acids and an increase in hydrocarbons. While methane is the only hydrocarbon observed to be produced in large quantities by bacteria, small amounts of paraffin hydrocarbons in the range of lubricating oil and wax have been shown by infrared and ultraviolet absorption studies to be produced by certain sulfate-reducing bacteria (193).

Ginsburg-Karagitscheva (194) regards it as established that petroliferous formations have been inhabited by active microflora. He reported that anaerobic bacteria from the Black Sea transformed albuminous materials and fatty substances by processes of hydrogenation, decarboxylation, and polymerization into oil-like products having a bituminous odor. Phenol and *p*-cresol, rather common constituents of crude oils, are produced by the action of bacteria on *l*-tyrosine (195). The production of benzene and benzoic acid from tyrosine and phenylalanine has been reported in the earlier literature, but this observation has not been amply confirmed. While there is incontrovertible evidence for the bacterial production of hydrocarbons besides methane and certain carotenoid pigments (196), there are no reasons for believing that bacteria have produced petroleum, although bacterial activity may have contributed to petroleum genesis in various ways, particularly by conditioning organic matter in marine sediments.

Bacterial oxidation of hydrocarbons.—The presence in marine sediments of bacteria which are endowed with the ability of attacking petroleum hydrocarbons (197) suggests that such bacteria may prevent the accumulation of oil in certain environments. From water, marine sediments, and oil-soaked soil nearly a hundred species of microorganisms representing thirty genera have been described which attack one or more types of hydrocarbons (160). Most of these organisms function only in the presence of free oxygen, but recently it has been demonstrated that hydrocarbons are attacked by anaerobic sulfate reducers (148, 158, 198). Such bacteria may have played an important role in the modification of petroleum in certain deposits.

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Scripps Institution of Oceanography
University of California, La Jolla, California

Contribution No. 331

Reprinted from Copeia, 1947, No. 3, September 12

LAMNA DITROPIS, NEW SPECIES, THE SALMON SHARK OF THE NORTH PACIFIC.[1]—A study of the "salmon shark" or "mackerel shark" of the North Pacific Ocean shows it to be a species of *Lamna* quite distinct from *L. nasus* (Bonnaterre) of the North Atlantic. It also appears to be separable from the species of the Southern Hemisphere. Unlike *Isurus,* from which it differs in the structure of the denticles and of the vertebral centra, as well as in the hitherto used character of the teeth, *Lamna* is a member of the pantemperate fauna, avoiding the tropics. We have in preparation a paper discussing these generic and distributional relationships, along with a detailed description and figures of the new species. This diagnosis is published now to make the name available for mention by Bigelow and Schroeder, in their treatment of the elasmobranchs in the forthcoming first volume of the *Fishes of the Western North Atlantic.*

Lamna ***ditropis,*** new species

Holotype.—An adult male collected in 300–350 feet of water 3.5 miles off the Beach Club at La Jolla, California, by Art Coles and Edgar E. Rock on December 7, 1945. Field No. H45-211, Cat. No. 36471, Museum of Comparative Zoology.

Range.—Coastal waters of the North Pacific, from San Diego, California, through the Pacific Northwest and Alaska to Japan. Generally in deeper waters southward.

Diagnosis.—Like *Lamna nasus* in most respects, differing most conspicuously in having the lower parts coarsely blotched with blackish in the adult and in having the snout broader and relatively shorter, particularly in the preoral length.

The often-copied figure of *Lamna cornubica* that appeared in Jordan and Evermann's *Fishes of North and Middle America* (Bull. U. S. Nat. Mus., 47 (4), 1900: 3232, pl. 6, fig. 22), was based on a young specimen of *Lamna ditropis* from Santa Cruz (not "Santa Barbara"), California. This specimen, Cat. No. 27368, U. S. National Museum, is designated as a paratype.—Carl L. Hubbs and W. I. Follett, *Scripps Institution of Oceanography, University of California, La Jolla, California,* and *California Academy of Sciences, San Francisco, California.*

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 331.

Contribution No. 332

ctions, American Geophysical Union Volume 28, Number 5 October 1947

RESEARCH WITHIN PHYSICAL OCEANOGRAPHY AND SUBMARINE GEOLOGY AT THE SCRIPPS INSTITUTION OF OCEANOGRAPHY DURING APRIL 1946 TO APRIL 1947

H. U. Sverdrup and Staff

(Contributions from the Scripps Institution of Oceanography, New Series, No. 332)

September 1946, Norris W. Rakestraw joined the staff of the Scripps Institution as Pro-
of Chemistry. He has been engaged in instruction and the planning of a research program
istry.

F. McEwen has completed the tabulation of a number of functions which repeatedly occur
iety of oceanographic problems. He continued his work on the theory of dispersion of
l in the sea from given area and volume sources, introducing different assumptions re-
initial conditions and coefficients of diffusion. Several of the theoretical results have been
to questions as to the dispersal of the radioactive material deposited in the water after
ic bomb explosion at Bikini.

earch work has been started on the dynamics of large horizontal eddies (axis vertical)
eristic of the ocean off southern California. Preliminary work based upon 1940 and 1941
tions indicated that after its formation such an eddy increases in area and decreases in
according to a solution of the hydrodynamic equations corresponding to an initial concen-
of vortex motion within a circular area of more than 10 km in diameter. The solution of
blem depended upon earlier work on diffusion from a circular area, and the numerical
quires the fundamental tables already computed for the diffusion problem. Extensive
entary tables have been computed for ready numerical application to specific problems of
from a circular area and the behavior of horizontal eddies.

major part of the research in physical oceanography and submarine geology has been
out under Navy contracts. This work comprises analyses of bathythermograph observa-
alysis of ocean currents, studies of sea and swell, and examination of beaches and sub-
topography in shallow water.

e F. Leipper is undertaking an examination of the relation between the meteorological con-
over the ocean and the thermal structure of the surface layer, but the very frequent oc-
e of internal waves of periods ranging from 10 or 15 minutes up to 24 hours makes it ex-
difficult to examine changes in the heat contents of the waters. A great amount of time
efore been spent in devising methods for eliminating the effect of internal waves.

r the coast off La Jolla large temperature fluctuations have been found which appear to be
o intense mixing which occurs when tidal currents flow over a very irregular bottom. In
, this mixing may bring water to the surface from such depths that locally the surface
ture may drop as much as six degrees centigrade within ten minutes. These features will
ined in detail. Leipper is also carrying out a study of methods for improving the fore-
of fog in coastal areas, making use of knowledge of sea-surface temperatures.

analysis of ocean currents undertaken by W. W. Wood has dealt with the statistical sig-
e of such average currents as are represented on different types of charts. An analysis
gress of variability in currents which may be apparent only because the observations are
from ships which may have crossed or followed a narrow current. The observed set in
may in such cases depend very much upon the course of the ship.

e studies of sea and swell by W. H. Munk and R. S. Arthur the concept that wind waves
ulsively generated has been a very fruitful one which has led to a better understanding of
rved characteristics of swell. The physical basis for the forecasting procedures which
eloped during the war is steadily being improved and at the same time a number of con-
have been arrived at which can be tested when suitable ovservations become available.

The theory of impulsively generated waves has also been applied successfully to tsunamis. appears possible that records of tsunamis can give information as to the extent in space and of the initial disturbances of the sea surface which generated the train of waves.

A. R. Champion has completed the installation at a depth of 40 feet of one recording wav off the Scripps Institution pier. Two other wave meters at depths of 120 and 600 feet will be stalled in the near future. These wave meters were built by the Department of Mechanical gineering at Berkeley. Work on analysers of wave records has been started in cooperation the Woods Hole Oceanographic Institution.

F. P. Shepard has carried out systematic studies of beach profiles at a number of locali in the vicinity of La Jolla and in connection with these studies has made records of breaker acteristics and of longshore currents. Detailed examinations of rip currents have been mad La Jolla. With the aid of a diver the heads of the canyons in the La Jolla area are being exam The Navy has placed a buoy boat at the disposal of the Institution and this is being equipped shallow recording sonic depth finder in order to undertake repeated surveys of the bottom to graphy in the La Jolla Bay. Special sand traps will be used to examine details of sand movem and compare findings with changes in the bottom topography.

The most gratifying development is the interest shown by young men in the study of ocea graphy. In the spring semester of 1947, 41 graduate students were registered at the Scripps Institution, including nine from other countries. Twenty-six of these students are specializi physical oceanography or submarine geology, and most of them participate in the different r projects in progress.

Scripps Institution of Oceanography,
University of California,
La Jolla, California

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Contribution No. 333

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VAVE EROSION ALONG THE SOUTHERN CALIFORNIA COAST

BY F. P. SHEPARD AND U. S. GRANT IV

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ABSTRACT

Vide wave-cut terraces along the southern California coast are apparently in
ord with the present stand of the sea and therefore must have been cut within
last few thousand years. Photographic comparisons, however, indicate that the
sion of rocky coasts has been negligible in the past 50 years even where the rocks
relatively soft shales. Narrow projecting points, stacks, and sea arches have
fered some erosion, but the straighter sections of rock cliffs look untouched. On
other hand, photographs and measurements indicate a retreat of unconsolidated
mations on the open coast of as much as a foot per year. The erosion of uncon-
idated materials near the Scripps Institution is going on at a decreasing rate judg-
from a comparison of three sets of measurements spaced over the past 28 years.

INTRODUCTION

)ld residents of coastal communities often express opinions that within a genera-
ı or two local sea cliffs have undergone great erosion. The reality of such erosion

is attested by the undermining of shore property during hurricanes like that of 193 on the east coast (Brown, 1939) and by tidal waves such as occurred on April 1946, in the Hawaiian Islands. Even ordinary storm waves may make deep inroa into a coast line so that owners of summer cottages may find that their homes ha been ruined by the retreat of the adjacent sea cliff during their absence in winte Figures of the rate of erosion of sea cliffs have, however, given somewhat erroneo impressions of the power and effect of wave attack because these figures do not a ways differentiate between easily eroded and resistant coastal formations. Th the rapid retreats during hurricanes and tidal waves, insofar as the writers kno have taken place only in unconsolidated formations.

Before unduly alarming owners of coastal property by tales of rapid cutting ba of cliffs one should give more consideration to the effect of waves on various typ of formations. Johnson (1925) called attention to the extremely variable erosi rates on the hard-rock and on the weak-rock coasts of New England and Acadi From his illustrations of weak-rock coasts of New Brunswick and Cape Bret Island one gathers that rapid wave erosion of weak rocks may be expected. To te the rate of erosion in weak-rock formations more completely the writers have c lected old photographs (some of them dating back to 1887) of the weak-rock coast cliffs in Southern California. These photographs were retaken, where possible, fro the same position to see what had happened in the interim. For comparative pu poses studies have been made of cliffs consisting of unconsolidated formations, soft Tertiary formations, of more resistant Cretaceous sandstones, and of other old formations. This investigation has been going on for the past 11 years, and it now possible to obtain information on erosion rates from many coastal areas whe old photographs were not available.

ACKNOWLEDGMENTS

Some of the field and photographic expenses were defrayed by a grant to t junior author from the Penrose Bequest of The Geological Society of Ameri Help was also received from the Scripps Institution and the University of Califor at Los Angeles. Numerous individuals provided the writers with old photograp which helped in determining the extent of erosion of the sea cliffs. This work rep sents in part the results of research carried out by the Hydrographic Office and t Bureau of Ships of the Navy Dept., under contract with the University of Ca fornia.

FACTORS INVOLVED IN WAVE EROSION OF ROCKY COASTS

HARDNESS OF THE ROCK

Soft Tertiary shales which are abundant along the California coast should easily eroded by the crystalline gravel and cobbles, which are available along ma beaches and can be thrown against the sea cliffs. At the other extreme are the cr talline rocks which are rare along the southern California coasts. Intermedi types such as sandstones may have relatively soft cement.

PLANES OF STRUCTURAL WEAKNESS

Rocks with many joint cracks or other openings in which waves can compress the air and cause explosive recoil are more subject to erosion than those which are relatively free from such openings.

COASTAL CONFIGURATION

Straight cliffs offer much less chance for successful wave attack than extremely rregular coasts where the waves can work into clefts and under arches and around stacks and projecting points.

SOLUBILITY OF ROCKS AND ROCK CEMENT

Solution is an important factor in cliff recession as has been shown by Emery 1941). Limestones and any rock with calcareous cement may be dissolved as a esult of the organisms living in tide pools or in the wet crevices of cliff faces. These rganisms, according to Emery (personal communication), increase the acidity of he water during the night so that solution of calcium carbonate may take place hereas normal sea water is too saturated to allow solution.

HEIGHT OF CLIFFS

High cliffs recede more slowly than low ones because the undercutting of the high liffs causes large landslides which in turn must be removed by the waves before ecession can continue. On the other hand the top of a high cliff may recede more apidly at least for a number of years because of the slides which take place.

NATURE OF WAVE ATTACK

There are many reasons for more concentrated wave attack on one part of a coast han another. Headlands are usually the loci of heavy wave attack because of ubmarine projections beyond the headlands which cause the waves to converge nd thus increase their height (Munk, 1947). Deep water adjacent to the coast, as r example a submarine valley, will result in wave divergence and in correspondingly w waves reaching the shore. The presence of reefs outside the coast will break e power of the waves particularly if there are deep-water zones between the reef nd the shore.

OBSERVED CHANGES

During the investigation of cliff erosion the writers attempted to locate the exact sition from which old photographs were obtained. To accomplish this ranges were ught near the left- and right-hand sides of the old photographs. Also objects in e foreground were checked with special care to make the duplication as close as ssible. When one considers that most pictures of sea cliffs are taken near the edge the cliff it is easy to see that any appreciable retreat would make it virtually possible to retake the photograph from the same point. Despite the fact that the w photographs were taken after an interval of from 29 to 59 years, it was necessary in only one place to duplicate the photograph by holding the camera out beyond t rock cliff.

Undoubted changes have been observed at a few places. All of these change however, have been either the toppling over of an arch (Pl. 1, figs. 1, 2), the remov of a stack (Pl. 1, figs. 3, 4), the partial collapse of the roof of a sea cave (Pl. 2, fig. or the development of a landslide which was not directly the result of wave actio

Cathedral Arch off La Jolla (Pl. 1, figs. 1, 2) was destroyed shortly after 190 Up to 1921 both buttresses of the arch were left standing; some time between 19 and 1937 the eastern buttress was removed. The remaining stack has undergo slight changes since that time. This erosion has taken place at a point where t waves converge because of a turn in the coast, although wave attack is somewh decreased by the ledges which protect the wave approach from the west. The ro is a massive, comparatively well cemented Cretaceous sandstone with a small numb of joints. The cement is calcareous. Similar collapse of an arch took place at Su set Cliffs on Point Loma between 1938 and 1940. The material here was crumb shale. Also a small shale arch collapsed a few miles north of La Jolla in 1941.

A photograph was taken in 1887 from the firmly cemented sandstone cliffs at t south side of Ocean Beach. The location is at a point of wave convergence and unprotected from the free sweep of the waves. The old photograph (Pl. 1, fig. showed a stack which is now completely eroded. Also the photograph was tak from another stack, where it was impossible to get a picture from exactly the sa position. However, retreat has not been very great and is largely confined to p jecting stacks.

South of Ocean Beach the road was constructed directly over a cave. The writ have known of this cave for 20 years. No trouble was experienced until the spr of 1946 when a partial roof collapse took place (Pl. 2, fig. 1). It does not seem lik that wave attack during this period had much if anything to do with the collap

Old photographs of the well-known caves which flank the north side of the Jolla Peninsula show that a collapse has taken place here also. The arch over cave gave away about 20 years ago. The rock here is also Cretaceous sandsto The water along the cliffs is about 10 feet deep, and waves do not ordinarily br with any force against the cliffs. The collapse may have been due to forces ot than waves although originally the caves were in all probability a wave produ

In contrast to these localities where changes were observed we have found innum able localities where there has been essentially no modification for half a centu Surprisingly, in localities where erosion appears to have been inconsequential, h sea cliffs, sea caves, and wide wave-cut platforms exposed at low tide all testify the importance of wave erosion in the past. Since it is unbelievable that the C fornia coast with its abundant raised and tilted terraces could have long stood s the finding of level benches exposed at low tide such as the one in Figure 2 of Pla must indicate a fairly rapid rate of erosion. It is unlikely that the sea level has st still more than a couple of thousand years. The low elevated terraces of the isla of the Pacific and most coasts of the world testify to the recent negative shift of level suggested by Daly (1920) and supported by most other investigators. If bench in Figure 2 of Plate 2 was formed in approximately 2000 years, the rat

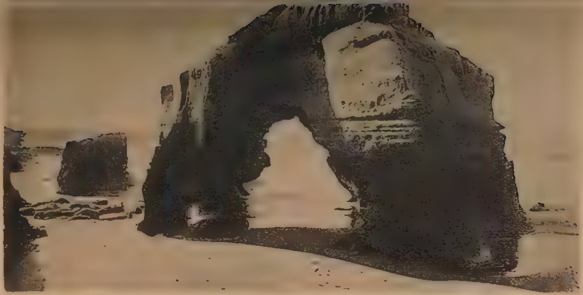

FIGURE 1. CATHEDRAL ARCH AT LA JOLLA IN 1900

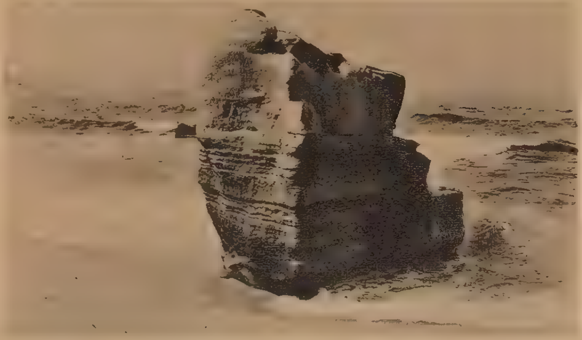

FIGURE 2. THE WESTERN BUTTRESS OF CATHEDRAL ARCH IN 1937

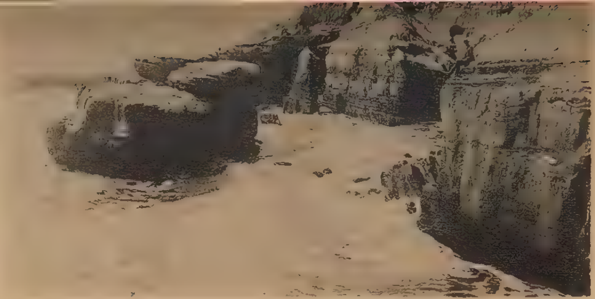

FIGURE 3. THE CLIFFS AT OCEAN BEACH IN 1887

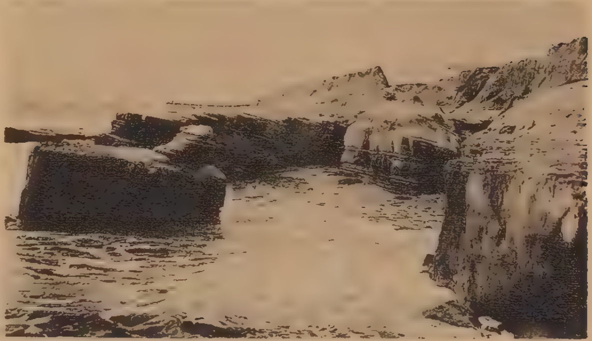

FIGURE 4. THE OCEAN BEACH CLIFFS FROM APPROXIMATELY THE SAME POSITION IN 1946.

Note the stack in center of figure 3 has disappeared, also the stack on the left has been considerably reduced, and the position from which the picture was taken could not be reached because of erosion of another stack. (Photo by W. F. Jewell.)

WAVE EROSION AT LA JOLLA AND OCEAN BEACH,
SAN DIEGO COUNTY

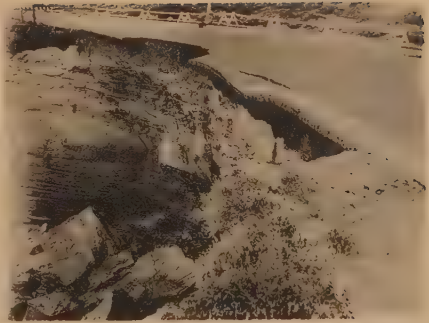

FIGURE 1. THE RECENTLY COLLAPSED ROOF OF A CAVE AT SUNSET CLIFFS WHICH HAS UNDERMINED THE ROAD.

The remnant of the cave extends for 60 feet under the road. (Photo by W. F. Jewell, April 1, 1946.)

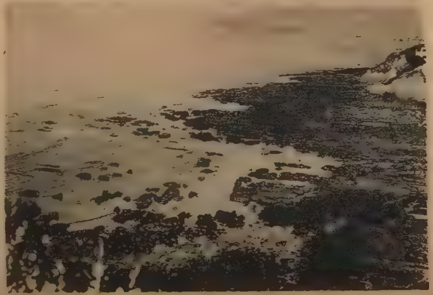

FIGURE 2. WAVE-CUT TERRACE EXPOSED AT LOW TIDE AT THE BASE OF THE 100 FOOT CLIFF JUST

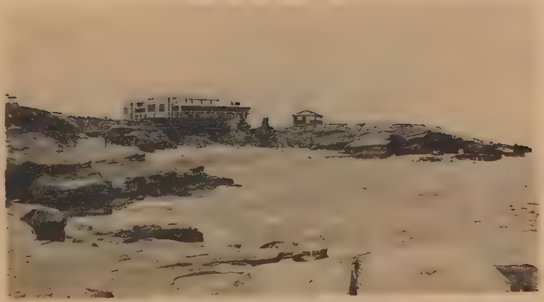

FIGURE 3. LA JOLLA COVE IN 1906
(Photo by Herbert R. Fitch.)

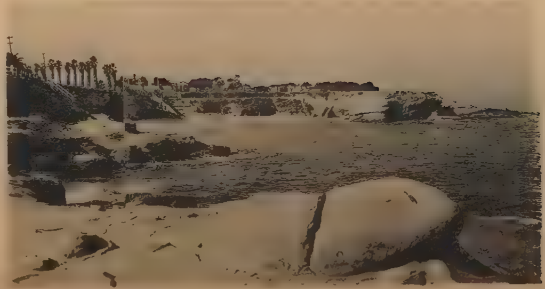

FIGURE 4. LA JOLLA COVE IN 1945.
Note the numerous concretions in the hard Cretaceous sandstone

sion must have averaged a foot in 4 years. This rate has not been maintained e no appreciable change can be seen in the past 40 years although slight cutting taken place locally, and landslides have occurred near the top of the cliffs.

The inconsequential rate of erosion of the Cretaceous sandstone around La Jolla ve in 40 years is shown in Figures 3 and 4 of Plate 2. Comparing the old and new

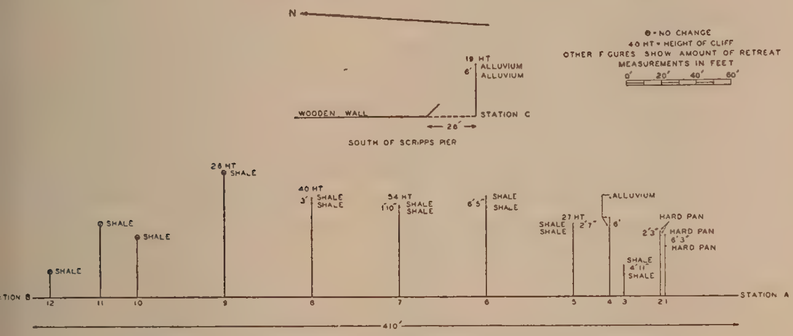
N
● = NO CHANGE
40 HT = HEIGHT OF CLIFF
OTHER FIGURES SHOW AMOUNT OF RETREAT
MEASUREMENTS IN FEET
0' 20' 40' 60'
19 HT
6'
ALLUVIUM
ALLUVIUM
WOODEN WALL
STATION C
26'
SOUTH OF SCRIPPS PIER
28 HT
SHALE
40 HT
3'
SHALE
SHALE
54 HT
1'10"
SHALE
SHALE
6'5"
SHALE
SHALE
ALLUVIUM
27 HT
SHALE
SHALE
2'7"
6'
HARD PAN
2'3"
HARD PAN
6'3"
HARD PAN
SHALE
4'11"
SHALE
SHALE
SHALE
SHALE
TION B
12
11
10
9
8
7
6
5
4
3
2
1
STATION A
410'

FIGURE 1.—*Measurements of sea cliffs near Scripps Institution*
For locations *see* Figure 3 of Plate 4.

tographs one can see the same concretions in the sandstone as were there at the lier date. One large boulder-like concretion has been shifted but has not yet n carried over the edge of the cliff. The rock is firm, but waves converge on both es of the cove and rise to considerable heights during winter storms when the swells coming from the northwest.

Two miles north of La Jolla, the Eocene shales, sandstones, and conglomerates ve not changed appreciably in 30 years (Pl. 3, figs. 1, 2) despite the relatively soft k. The difference in the foreground of the photographs is due to the sand fill ich is a seasonal effect. The old photo was taken after a period of large swells. e outlying rocks which are part of a diabase dike running diagonal to the coast have tected the cliffs to a considerable extent. The cliff face just to the right of the yon is north of the dike and cannot have retreated to any extent since the same ck that was visible 30 years ago is still there although considerably widened. The e rocks in the surf look the same, and various other rocks below the cliff can be ognized in the two pictures. Other photographs, not shown here, indicate that ails of the cliff base have remained unchanged and that the projecting concretions 30 years ago are still present. On the other hand, farther south near the Scripps titution pier some projecting shale masses have been cut back, in one instance as ch as 6 feet, in the past 10 years (Fig. 1). This shale is so soft that it can be dug h one's fingernails. However, even this soft shale has retreated only at the south- end of the measured line. Four stations showed no retreat in 10 years at the thern end. To the south the waves are commonly higher than to the north . 4, fig. 3).

hotographic comparisons at the Point Fermin lighthouse, just west of the port San Pedro (Pl. 3, figs. 3, 4), show that in 42 years the shale cliffs at this point have undergone almost no change. Many of the rock projections of the past cen can still be seen in the recent photograph. Even some of the rocks projectin from the sea floor can be recognized. The cliffs are somewhat protected by beds. Also the offlying island of Catalina protects the area from southwest storms, and northwest swells hit the coast diagonally so that they do not hav much of an impact as in localities farther around the point to the west. At P Vicente which is west of Point Fermin reports of retreating rock cliffs are curr but the writers' photographs of the past 10 years show no appreciable chan East of the Point Fermin light, however, there is an area where landslides are ceeding slowly and causing considerable trouble to the city highway commiss

North of Point Conception, where the California coast makes a large bend, chan from an east-west to a north-south direction, the ocean swells are almost invari larger than to the south of the Point. It could therefore be anticipated that ero would proceed more rapidly in this area. Some checks have been made of the ero in the vicinity of Port San Luis 50 miles north of Point Conception. Photogr taken here by George W. Stose before May 1898 have been retaken. Plate 4 sh a comparison on the open coast north of Port San Luis. A few outlying rocks s as some protection in this area, and kelp beds are found outside. However, the w must have considerable power of attack in the area as there are no outlying isla Accordingly it is amazing to find that the details of the cliffs and of the stacks virtually the same after approximately 50 years. Many of the rocks in the s cove in the foreground can be matched. One even gets the impression that the vium has undergone virtually no cutting in the half-century interval. The ret of the alluvium insofar as waves are concerned is impeded by the underlying masses. Another Stose photograph south of Port San Luis showing elevated w cut terraces can also be matched detail for detail with no appreciable change. sibly these cases are exceptional. If more old photographs could be found in northern area a different story might result. On the other hand several photogr were made about 10 years ago, and some of these have been retaken showing failure of a decade to produce significant inroad into the irregular coastal cut in moderately resistant Franciscan rocks.

The above evidence provides no data which would allow an estimate of the pre rate of retreat of rocky cliffs in southern California. The cliffs show no sign systematic retreat. Accordingly one wonders if rates of retreat of rock cliffs been established in other areas on thoroughly reliable evidence. Could these also be explained largely by collapse of caves and sea arches? Conversations correspondence with foreign geologists suggest that some of the cliff retreats cite the literature are based on very insecure foundations. Historical records, old sketc and old photographs in the European area should be restudied to determine authenticity of postulated cliff retreat in that region.

WAVE EROSION IN UNCONSOLIDATED ALLUVIUM

Cliffs consisting of Recent or Pleistocene alluvial formations along the Califo coast have a very different history from the cliffs consisting of solid rock. The complete record of erosion has been kept at the Scripps Institution. At the be

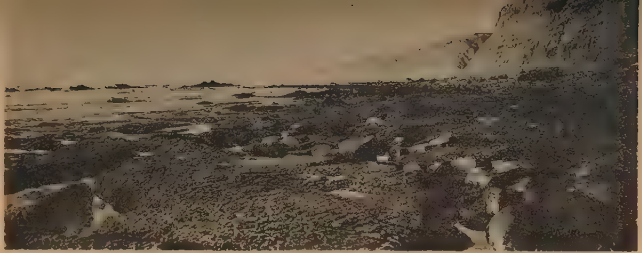

Figure 1. View of Eocene Shale and Sandstone Cliffs North of Scripps Institution
Taken about 1916. The lack of sand under the cliffs indicates that the picture was taken after a period of heavy surf.

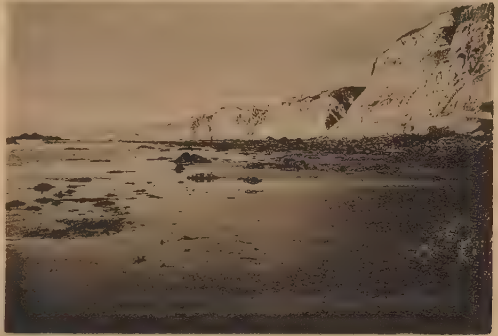

Figure 2. View from the Same Spot as Figure 1
Taken in November, 1945. Note that numerous outlying rocks can be matched in the two photos, and that the crack in the cliff to the right of the canyon has widened, but the block has survived 30 years of weathering. The sand cover in the foreground typefies periods of small surf. (Photo by U. S. Grant IV.)

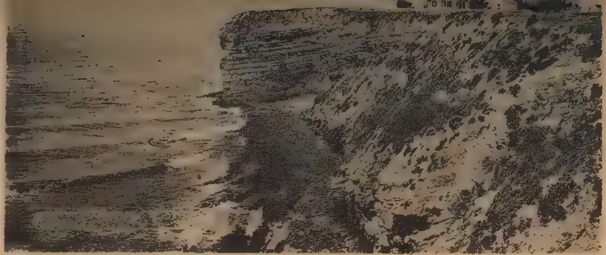

Figure 3. Sea Cliffs at Point Fermin, West of San Pedro
Taken in 1898

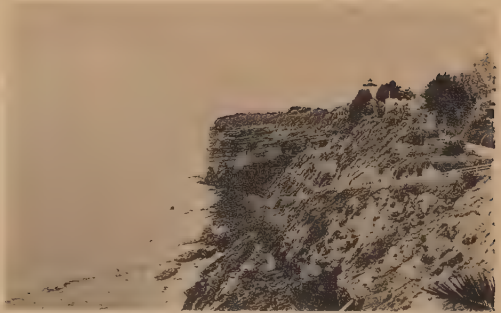

Figure 4. View from Same Spot
Taken in 1940. Note that the cliffs show little sign of change, and the rocks beneath the cliff can be matched in some places. (Photo by U. S. Grant IV.)

RELATIVELY STABLE HIGH CLIFFS NEAR LA JOLLA AND AT POINT FERMIN

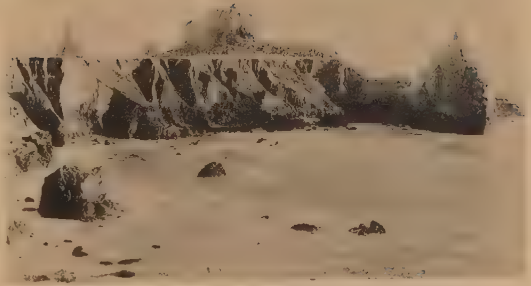

FIGURE 1. SEA CLIFF NORTH OF PORT SAN LUIS
Taken prior to 1898. (Photo by George W. Stose.)

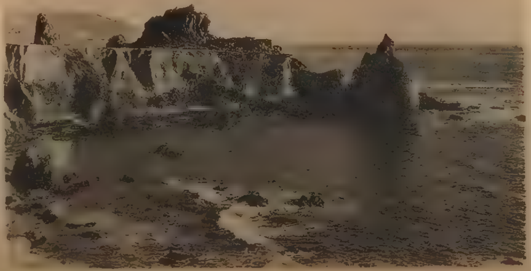

FIGURE 2. VIEW FROM SAME SPOT
Retaken in 1945. Note the almost complete absence of change

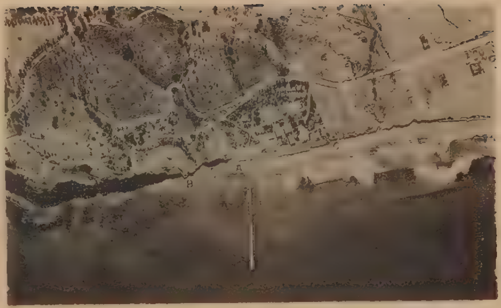

FIGURE 3. AIR VIEW OF THE SEA COAST IN THE VICINITY OF SCRIPPS INSTITUTION
"A," "B" and "C" refer to positions on the map of Figure 1. Note the variation in width of the surf zone along the coast and the small breakers inside the reef shown to the left of "B." (Official photograph of U. S. Navy, 1945.)

g of the record the recession of the recent alluvial cliffs north and south of the
titution proceeded at the rate of 1.5 feet per year for a period of 11 years; during
next 7 years the retreat was cut down to 1.0 foot per year, and in the past 10
rs it has been reduced again to about 0.6 foot per year. An exact survey was
de in 1936 and was remeasured using the same bench marks for the extreme ends
he line (Fig. 1). Unfortunately not many points on the alluvium were measured
viously, but each of the three stations measured shows approximately 6 feet of
sion. The waves attack the cliff only at high tide and only after the winter storms
e cut away the beach berm which is built out in front of the cliffs every summer.
sion of the cliffs is facilitated by the burrows of rodents; the burrows are greatly
rged during heavy rains and develop sizable openings on the cliff faces.

he retreat of the alluvium north of the Scripps Institution is also shown in a
tographic record (Pl. 5, figs. 1, 2). Here the cliff has been lowered as it has
eated into a valley. The scale in Figure 2 of Plate 5 will give some idea of the
year retreat. Also the position of the cliff is indicated by the white line in Figure
f Plate 5. Pictures taken at intermediate dates reveal the authenticity of this
parison. The elongate pipelike concretions on the beach can be seen in both
tographs although they were partly hidden in the early picture. It will be noted
t the end of one concretion has been broken off and removed.

nother example of erosion in alluvial material is illustrated in Figures 3 and 4
Plate 5 which show the rapid retreat of the low sea cliffs at Coronado. This ero-
n was produced by large waves, but an underlying cause may have been the build-
of the Zuninga (or San Diego) jetty at the west end of North Island. This jetty
ubble-stone construction was built by the Federal government to facilitate natural
ur of the bar at the entrance of San Diego Bay. Construction began in October
3 and continued intermittently until its completion in July 1904. The final length
7500 feet, and its seaward end was in a depth of 30 feet of water. According
data obtained during a study of beach erosion at Coronado by Colonel C. T.
ds, the jetty first produced beach erosion along North Island. As the jetty length-
d, this erosion made its effect apparent progressively eastward until in 1905
e attack during winter storms, particularly in March, produced the disastrous
cts shown in Figures 3 and 4 of Plate 5.

recent series of large waves at Sandyland, 10 miles east of Santa Barbara,
led low alluvial cliffs and undermined houses at the point shown in figure 4 of
e 4. The damage seems to have been due in large part to the Santa Barbara
kwater which depleted the supply of sand which was previously drifting along
coast. The net result was the removal of the sand beach from in front of the
s, allowing cliff erosion.

he retreat of alluvial cliffs in southern California can be matched in numerous
r areas. Probably the bulk of the instances of cliff retreat listed by Johnson
9, p. 65–72) are examples of retreat in unconsolidated formations. The U. S.
st and Geodetic Survey measured the retreat on the exposed outer coast of Cape
in glacial outwash deposits and found that for 40 years it averaged 3.2 feet per
(Johnson, 1925, p. 400). At Winthrop Head, Boston Harbor, the retreat in
ears has averaged 9 inches per year and about the same at Grover's Cliff (John-

son, 1925, p. 400). All these cliffs are from 50 to 100 feet high. Rates of 5 or 6 fe per year are reported from glacial-till cliffs of Lake Michigan (Johnson, 1925, p. 40 Unfortunately some of these studies of cliff retreat date back to the last century, a it is difficult to check their reliability.

CONCLUSIONS

Investigations, largely by comparing old photographs, have shown that erosion rock cliffs in southern California has been negligible during the last few decad This slight erosion contrasts strangely with indications of extensive erosion duri the past few thousand years. The contrast may be explained partly by a decreasi rate as the cliffs retreat and terraces beneath the cliffs grow wider. This may be fundamental importance. Possibly waves are not so large along this coast as w formerly the case. A third possibility is that significant erosion takes place on ra occasions, and there has been no such occasion since the old photographs we taken.

Erosion of the unconsolidated alluvium has, unlike the rock, proceeded with co siderable regularity. The measurements at Scripps Institution, however, show th the rate has been decreasing although there is no evidence to show that this decrea is not related to decreasing wave height. A retreat of a foot a year appears to common in southern California and is probably exceeded in other areas where wav are larger.

The evidence from southern California suggests that the danger of coast erosi in areas of rock cliffs may not be great, but that rapid erosion can be anticipat where no appreciable beaches front cliffs of alluvium. Studies in other areas a desirable before these conclusions should be applied too widely.

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Scripps Institution of Oceanography, La Jolla, California; University of California, Los Angeles, C fornia.

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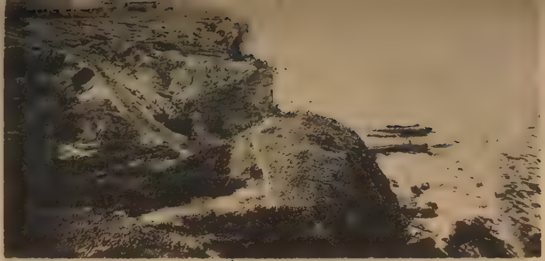

FIGURE 1. PHOTOGRAPH OF THE SEA CLIFFS AT SCRIPPS INSTITUTION TAKEN IN 1913
The white line shows the approximate position of the present cliffs.

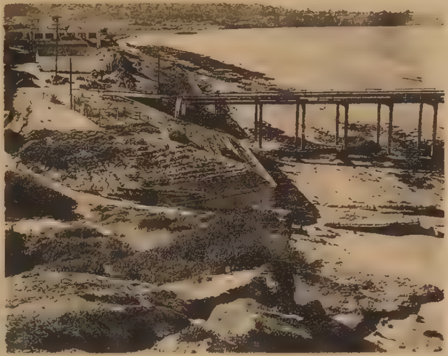

FIGURE 2. PHOTOGRAPH FROM THE SAME LOCATION IN 1945
Note that the sea walls do not protect the alluvial cliffs in the foreground. Scale given in feet.

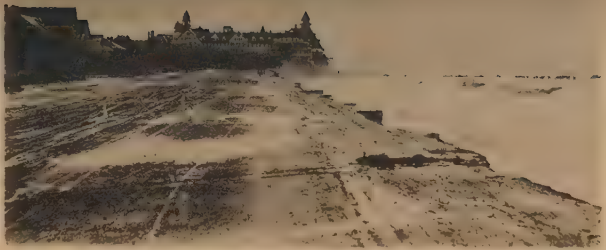

FIGURE 3. STORM WAVES ACTIVELY ERODING ALLUVIAL CLIFFS AT CORONADO
The Coronado Hotel shown in the background. (Photo taken on February 6, 1905.)

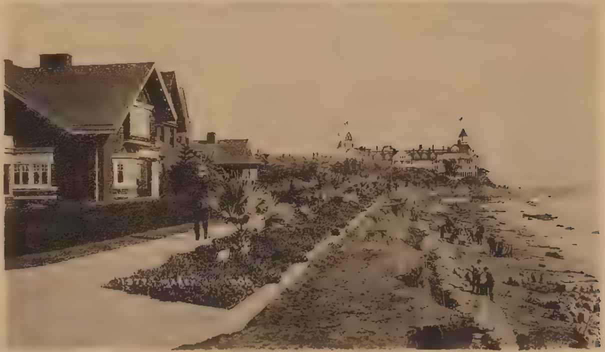

FIGURE 4. PHOTOGRAPH OF SAME AREA TAKEN MARCH 17, 1905 AFTER SEVERE STORMS
Note that the road in front of the houses had almost completely disappeared.

RETREAT OF ALLUVIAL SEA CLIFFS IN
SAN DIEGO COUNTY

Contribution No. 334

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MICROBIAL TRANSFORMATION OF MOLECULAR HYDROGEN IN MARINE SEDIMENTS, WITH PARTICULAR REFERENCE TO PETROLEUM[1]

CLAUDE E. ZOBELL[2]
La Jolla, California

ABSTRACT

Molecular hydrogen is produced by a large number of bacterial species, many of which occur n marine sediments. Such bacteria have been demonstrated in marine bottom deposits, oil-bearing ands, and in reservoir fluids from oil wells. Up to 10,000 hydrogen-producing bacteria were found per ram of mud from the floor of the Pacific Ocean. Pure or enrichment cultures of such bacteria have een shown to liberate hydrogen from organic compounds at temperatures ranging from near 0° C. o as high as 65° C. Hydrogen is liberated from virtually all kinds of organic compounds, and most eadily from carbohydrates or polyhydroxy alcohols. Redox potentials more reducing than E_h -0.05 olt and reactions ranging from pH 5.5 to 9.8 favor hydrogen formation. It is possible to demonstrate he production of hydrogen in samples of marine mud by inhibiting the activities of hydrogen-oxidiz- ng bacteria. The latter are believed to account for the general exiguity or lack of molecular hydrogen n marsh gas and other natural gases, although traces of hydrogen have been reported in such gases.

The rapid consumption of hydrogen by samples of soil and sediments is attributed to the activi- ies of bacteria or their enzymes which catalyze its oxidation. Listed are several species of autotrophic erobes which oxidize hydrogen to water. Of greater geological importance are various kinds of naerobes which oxidize hydrogen with the formation of methane, simple organic acids, ammonia, nd hydrogen sulphide. Evidence is presented that bacteria produce methane by catalyzing the re- uction of carbon dioxide or other one-carbon-atom compounds with hydrogen. Other types of bac- eria catalyze the reduction of carbon dioxide by hydrogen with the formation of formic, acetic, and ossibly other carboxylic acids. Amino acids and other organic compounds are also reduced by hy- rogen-activating bacteria. Certain bacteria found in sediments utilize energy from the oxidation of olecular hydrogen for the reduction of sulphate. Others reduce nitrate and nitrite.

The hypothesis is advanced that various kinds of hydrogen-oxidizing bacteria, in conjunction ith radioactivity and other catalytic agents in sediments, may contribute to the formation of petro- um hydrocarbons. Different sources of hydrogen and the energetics of some hypothetical reactions re considered.

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[2] Scripps Institution of Oceanography, University of California. The writer acknowledges the nstructive criticisms and suggestions of W. D. Rosenfeld, W. E. Hanson, B. Hubbard, and Clark oodman. The technical assistance of W. E. Hutton, G. D. Novelli, Josephine B. Senn, D. M. Upde- aff, Helen H. Whelply, and Jean S. ZoBell is also acknowledged. Thanks are also due to members the A.P.I. advisory and reviewing committees who have contributed to the preparation of this per in various ways.

INTRODUCTION

It has been known for some time that there are species of bacteria which produce and others which utilize molecular hydrogen. Bacteria and allied microörganisms which are able to produce free hydrogen from a large variety of organic substances appear to be rather widely distributed in nature. Also widespread in occurrence are microbial species which activate the combination of molecular hydrogen with various organic and inorganic compounds. The activities of such organisms may help to account for the presence or absence of free hydrogen in source sediments of petroleum, they may contribute to the hydrogenation of organic matter, and they may play an important role in the origin of oil. Evidence for these pretensions is summarized on the following pages.

EARLY OBSERVATIONS ON HYDROGEN FORMATION

Historical.—The ability of bacteria to produce free hydrogen during the fermentation of organic compounds is well documented, dating from 1875 when Popoff (133) reported that mixed cultures from pond mud liberated hydrogen from calcium formate and cellulosic materials. A year later Fitz (51) demonstrated the production of hydrogen from the fermentation of glycerol. At nearly the same time, Hoppe-Seyler (83) showed that hydrogen resulted from the fermentation of calcium formate:

$$Ca(COOH)_2 + H_2O = CaCO_3 + CO_2 + 2H_2$$

He observed that, while methane and carbon dioxide were the principal products resulting from the fermentation of cellulose by mixed cultures, hydrogen was sometimes liberated, particularly in the early stages of fermentation (84, 85).

Tappeiner (163) was undecided as to whether observed differences in proportions of hydrogen and methane in gases evolved from fermenting cellulose were due to differences in the bacterial flora or to differences in experimental conditions, although it is now known that molecular hydrogen may be converted into methane. In 1883 Tappeiner (164) observed the production of varying proportions of hydrogen, methane, and carbon dioxide from the anaerobic decomposition of vegetable material inoculated with the intestinal contents of an ox.

Early workers observed that, whereas the gaseous products of fermentation by mixed cultures generally contained variable mixtures of methane and hydrogen, pure cultures produced either methane or hydrogen but not both gases. Pure cultures of two anaerobes, *Bacillus polymyxa* and *Vibrio rugola*, were found by Prazmowski (136) to ferment cellulose with the formation of hydrogen and carbon dioxide. In 1877 van Tieghem (175) noted the fermentation of cellulose by *Bacillus amylobacter* with the formation of hydrogen, carbon dioxide, and organic acids but no methane. In 1895 Duclaux (43) reported the formation of hydrogen by pure cultures of *Amylobacter butylicus* fermenting lactic acid, lactose, sucrose, starch, mannitol, and glycerol. He also observed the production of hydrogen by *Amylobacter ethylicus*.

The production of hydrogen and carbon dioxide in equimolar proportions by pure cultures of *Bacillus ethaceticus* was observed in 1891 by Frankland and coworkers to result from the fermentation of calcium glycerate (53), mannitol and dulcitol (54), dextrose (55), and arabinose (56), leading these workers to deduce that the gases resulted from the decomposition of formic acid, a by-product of fermentation:

$$HCOOH = CO_2 + H_2.$$

Recent observations summarized by Stephenson (156) have established that formic acid is a common by-product resulting from the fermentation of a large variety of organic compounds and that an enzyme, hydrogenlyase, splits formic acid with the formation of carbon dioxide and hydrogen. Hydrogen is also produced by other mechanisms.

In 1897 Omelianski (121) showed that hydrogen-producing and methane-producing bacteria are often closely associated in cellulosic materials undergoing fermentation in nature. By heating mixed cultures in the early stages of development to 75°C. for 15 minutes, a treatment which killed the vegetative cells of the methane producer without injuring the more slowly developing spores of the hydrogen producer, Omelianski (122) obtained from river mud, soil, and horse dung cultures of *Bacillus fossicularum* which produced hydrogen but no methane from cellulose. He gave the following balance sheet for the fermentation of cellulose by *Bacillus fossicularum:*

	Grams		*Grams*
Cellulose added	3.4743	Hydrogen produced	0.1038
Cellulose left	0.1272	Unidentified products	0.1309
		Carbon dioxide	0.9722
Cellulose fermented	3.3471	Fatty acids produced	2.1402
		Total	3.3471

The fatty acids consisted mostly of acetic and butyric acids with lesser amounts of valeric acid.

Review of literature on hydrogen producers.—Bacteria which produce hydrogen during the fermentation of fatty acids, sugars, starches, cellulose, pectin, peptone, amino acids, or other organic compounds have been demonstrated in river or pond mud (37, 78, 84, 85, 133, 160), lake mud (3, 36, 44, 162), marine mud (21, 30, 129, 143), soil (1, 9, 122, 171, 179), swamps (36, 72, 150), dead leaves (111), horse manure (78, 137), human feces (96), septic tanks (52, 138), sewage sludge (7, 29, 114, 166), retting flax (161), oil sands (62), and elsewhere in nature (29, 171).

Several bacterial species, which have been shown to be able to produce molecular hydrogen from a variety of organic compounds, are listed in Table I. The tabulation is by no means complete. Many bacterial species besides those listed in Table I are known to produce hydrogen (143). No one has ever made an exhaustive study of the ability of bacteria to produce hydrogen. This listing should suffice, however, to indicate that such ability is fairly common among anaerobic bacteria.

TABLE I

Some Microörganisms Which Have Been Reported in Literature to Produce Molecular Hydrogen from Various Substrates

*Name of Organism**	*Substrate from Which Hydrogen Was Liberated*
Aerobacter aerogenes	Glucose (97 152), glycerol (69), mannitol (70)
Aerobacter cloacae	Glucose (97, 152)
Aerobacter indologenes	Acetic, citric and succinic acids (24)
Bacillus acetoethylicus	Glucose (153)
Bacillus polymyxa	Cellulose (136), glucose (153)
Clostridium acetobutylicum	Amygdalin, cellobiose, galactose, glucose, fructose, lactose, maltose, mannose, salicin, sucrose (27), arabinose, gluconic acid, mannitol (88)
Clostridium butylicum	Aesculin, amygdalin, arabinose, cellobiose, dextrin, dimethyl glucoside, glucose, glycerol, inositol, inulin, maltose, melibiose, raffinose, rhamnose, starch, pyruvic acid, sucrose, trehalose, xylose (127)
Clostridium butyricum	Amygdalin, cellobiose, fructose, lactose, maltose, mannose, pyruvic acid, salicin, sucrose (27), pectin (97), arabinose, galactose, glucose, pectin, xylose (151), acetic, butyric, lactic and valeric acids, pectin (161)
Clostridium botulinum	Peptone (4), pyruvic acid (34), fructose, glucose, maltose, mannose, salicin, sucrose (173)
Clostridium hydrogenicus	Cellulose (180)
Clostridium celluloslytique	Cellulose (180)
Clostridium cellulosolvens	Cellulose (38)
Clostridium dissolvens	Cellulose (5, 96)
Clostridium fossicularum	Cellulose (5, 121, 122, 180)
Clostridium oedematis-maligni	Fructose, glucose, maltose, mannose, salicin, sorbitol, sucrose (173)
Clostridium sporogenes	Glucose (28, 71, 82), peptone (28, 71), glycerol, inulin, lactose, salicin, starch, sucrose (28)
Clostridium tetani	Aspartic acid, glutamic acid, serine (35), glucose (185)
Clostridium tetanomorphum	Glutamic acid (9), aspartic acid, cystine, fumaric acid, glucose, maltose, methionine, pyruvic acid, histidine, malic acid, serine, tyrosine, glycerol (188)
Clostridium thermosaccharolyticum	Glucose, xylose (147)
Clostridium welchii	Glucose, lactose (185)
Clostridium werni	Cellulose (180)
Escherichia coli	Mannitol (64, 68), arabinose, fructose, galactose (68), formic acid, glucose (68, 126, 167, 168), formic acid, glycolic acid (92), glucose (97, 152), fructose, glucose, maltose, mannose, salicin, sorbitol, sucrose (173), lactose (185)
Proteus mirabilis	Glucose (152)
Proteus vulgaris	Cystine (165), glucose (152)
Pseudomonas rathonis	Raffinose (101, 180)
Salmonella enteritidis	Glycolic acid (92)
Sarcina maxima	Fructose, glucose (148)
Sarcina ventriculata	Fructose (148), glucose (97, 148)
Serratia marcescens	Glucose (130)

* The generic and species names of organisms are those used by the respective authors whose works are cited in this article.

OCCURRENCE OF HYDROGEN PRODUCERS IN MARINE SEDIMENTS

Experimental methods.—Sea water enriched with 0.1 per cent each of K_2HPO_4, $NaHCO_3$, $(NH_4)_2SO_4$, and $Na_2S \cdot 9H_2O$ and 0.5 per cent of either glycerol, peptone, or shredded cellulose was used to demonstrate the presence of hydrogen-producing bacteria in samples of sedimentary material from various sources (143). After sterilizing the medium by heating in an autoclave for 20 minutes at 121°C. and adjusting the reaction to pH 7.2 with sterile solutions of NaOH and HCl, the medium was inoculated with a portion of the sample to be tested. In all manipulations precautions were exercised to avoid contamination and to preclude free oxygen. The function of the $Na_2S \cdot 9H_2O$ was to create anaerobic conditions and to maintain a low redox potential (195) which favors hydrogen formation.

The medium was dispersed for sterilization in bottles or flasks filled to capacity and stoppered with a one-hole rubber stopper. The latter was connected with a capillary glass tube bent to conduct evolved gases from the culture receptacle to a bottle or test tube filled with salt solution and inverted in a 22 per cent NaCl solution, which served as a confining liquid for the gas sample, as recommended by Dennis and Nichols (40). The inoculated media were incubated at 27°C. The quantity of gas evolved from day to day could be observed by noting the displacement of the confining liquid from the graduated bottle or tube into which the gas was discharged.

A second type of apparatus proved to be more satisfactory for detecting small quantities of gas produced by bacteria in culture media. It consisted of a culture receptacle, filled to capacity with medium and stoppered with a two-hole rubber stopper. One hole was fitted with a U-shaped glass tube extending to the bottom of the culture receptacle through which medium was forced into the overflow container as gas was produced. The other hole in the rubber stopper was fitted with a short length of tapered glass tube closed on top with a sleeve-type serum-bottle stopper having a soft rubber diaphragm through which a sterile hypodermic needle could be inserted for injecting inocula or chemical reagents or for removing samples of evolved gas with a syringe, according to the method described by Senn (142).

It is recognized that the diffusability of hydrogen through rubber and the solubility of gases in water constitutes two potential sources of error. Controlled experiments with all-glass apparatus have proved that the error is relatively small or actually negligible from the loss of hydrogen by diffusion. Hydrogen is soluble to the extent of 1.69 cc. per 100 cc. of water at 27°C., less in culture medium, and considerably less in 22 per cent NaCl solution, which was used in some experiments as the confining liquid. Therefore, any hydrogen gas liberated would be in excess of that required to saturate the culture medium or the confining liquid. The solubility of methane is 8.03 cc. per liter of water at 27°C. Its solubility in culture medium, like the solubility of other gases, depends primarily upon the salt concentration. The solubility of carbon dioxide is primarily a function of the pH of the medium, which may change during incubation of cultures, but error from this source is not great because the medium was well buffered at around pH 7.2 and it was virtually saturated with carbon dioxide at the beginning of the experiment. The solubility of the gases was estimated in the calculation of results when the volume of evolved gas was small, but, in most experiments, the volume of evolved gases was relatively large as compared to the amount of dissolved gas.

The composition of the gas was determined with an Orsat-type gas analyzer in most of the experiments.

Hydrogen producers in recent sediments.—Table II characterizes several samples of sedimentary materials in which hydrogen producers were demonstrated. Approximately one gram of the sedimentary material was used to inoculate 160 cc. of culture medium enriched with 0.5 per cent each of glycerol, peptone, and cellulose. In order to facilitate the comparison of results, the composition of the evolved gases is reported as if it consisted exclusively of carbon dioxide, methane, and hydrogen, although small quantities of nitrogen, hydrogen sulphide, and ammonia were usually present. There was no evidence for the production of carbon monoxide and no volatile hydrocarbon besides methane could be detected in any of the experiments.

TABLE II

Relative Proportions of Carbon Dioxide, Methane, and Hydrogen in Gases Evolved During Initial Stages of Anaerobic Decomposition of Cellulose, Peptone, or Glycerol by Bacteria Present in Approximately One-Gram Samples of Various Sedimentary Materials (Adapted from Senn, 143)

Sample No.	*Description of Sample*	*Percentage*		
		CO_2	*CH_4*	*H_2*
XXIX: 117-2	Organic-rich mud from Rozel Point, Great Salt Lake, Utah	94.6	0.6	4.8
XXIX: 117-3	Sand and muddy silt from Rozel Point, Great Salt Lake, Utah	50.3	1.0	48.7
XXIX: 125-1	Mud from swamp, La Coloma, Pinar del Rio, Cuba, sent by Standard Oil Co. of Cuba	90.5	0	9.5
XXIX: 125-2	Mud from swamp, Punta Gatos, Cuba, sent by Standard Oil Co. of Cuba	58.8	0	41.2
XXIX: 125-3	Mud from Ensenada Las Tunas, Cuba, sent by Standard Oil Co. of Cuba	70.1	0.6	29.3
XXIX: 125-4	Mud from near Guanimar, Pinar del Rio, Cuba, sent by Standard Oil Company of Cuba	60.1	0.7	39.2
XXX: 100	Marine mud from depth of about 2 feet, Mission Bay, San Diego, California	36.3	62.2	1.5
XXX: 102	Marine mud from water depth of 635 fathoms, from San Diego Trough	6.4	90.1	3.5
XXX: 114	Mud from shallow brackish water, Sorrento Slough, near Del Mar, California	31.6	65.2	3.2
XXX: 154	Sediment containing decomposing wood in sea-water tank, La Jolla, California	29.7	68.8	1.5
XXX: 190B	Mud from shallow brackish water, San Diego Bay, near Chula Vista, California	31.1	66.0	2.9
XXX: 190S	Mud from shallow brackish water, San Diego Bay, near Chula Vista, California	34.3	62.2	3.5
XXX: 192F	Marine mud core about 4 feet long, from 900 fathoms of water offshore from San Diego	26.6	71.7	1.7

Since the composition of the evolved gases varied with the period of incubation and other experimental conditions, the only significance that can be attached to the data in Table II is that hydrogen-producing microörganisms were present in the samples with which the media were inoculated. Negative results, of which there were many, are not reported. The absence of hydrogen in evolved gases does not necessarily indicate that no hydrogen was produced, because the amount produced may be inadequate to saturate the medium, or hydrogen may be oxidized by bacteria in mixed cultures about as fast as it is produced. The oxidation of hydrogen is suggested by the demonstrated presence of various kinds of hydrogen oxidizers in sediment samples and by the observation that the first gas evolved generally contained the highest percentage of hydrogen.

Attention is directed to the results obtained with the four Cuban mud samples numbered XXIX: 125 in Table II. These samples, which were collected for another purpose, had been treated with 25 per cent butyl alcohol as a preservative, but in spite of this treatment, spore-forming hydrogen producers survived. Methane producers, which are believed to oxidize hydrogen with the formation of methane, were inhibited or killed by the butyl alcohol. The occurrence of both types of bacteria in the Cuban mud was demonstrated in unpreserved samples of the same mud. The mixed microflora in the unpreserved mud fermented the medium with the formation of gas containing much more methane than hydrogen. The percentage of methane continued to increase while the carbon dioxide content of the gas decreased with prolonged incubation. The changing composition of the gas, which is generally observed with mixed cultures, is attributed to the reduction of carbon dioxide to methane by hydrogen. Hydrogen may also be oxidized by sulphate reducers and other types of bacteria.

By eliminating or inhibiting methane producers by various selective culture technics described by Omelianski (121, 122) and Mazé (111), the resulting cultures produced gas consisting primarily of hydrogen and carbon dioxide. Such enrichment cultures of hydrogen producers have been obtained from marine mud sample XXX: 192F by successively heating young subcultures to 80°C. for ten minutes. Spores of methane producers as well as hydrogen producers survived this treatment, but since methane producers germinated more rapidly, they were selectively eliminated by a repetition of the heat treatment. The gas produced by such an enrichment culture has been found to contain as much as 50 per cent hydrogen during the fermentation of glycerol or glucose.

Hydrogen producers in reservoir fluids.—The presence of hydrogen-producing bacteria in samples of reservoir fluids from oil wells was demonstrated by inoculating 150 cc. of nutrient medium containing 0.5 per cent each of glycerol, glucose, and cellulose with 10 cc. of oil or brine. After incubation for a week or two, about half of the samples tested provoked the formation of gas. The first gas produced was examined for the presence of hydrogen. The samples of reservoir fluids in which hydrogen producers were found are described in Table III.

Finding hydrogen producers in reservoir fluids from fourteen different oil wells is highly suggestive, but such findings are not conclusive because the bacteria might have been introduced in the formation when the well was drilled, or subsequently. Moreover, many of the samples may have been contaminated at the time of sampling, but if so, they were contaminated by bacterial types not commonly found in soil or fresh-water environments (196).

Methane producers were found in all samples of reservoir fluids and recent marine sediments in which hydrogen producers were demonstrated and in many samples in which hydrogen producers could not be demonstrated. Sulphate reducers were also found in such samples. Ginsburg-Karagitscheva (62) found hydrogen producers, methane producers, and sulphate reducers in fifteen samples of oil sands from the Grozny oil-field formation. Cellulose fermenters were also present (62).

Oil-well brine sample No. XXIX: 61 described in Table III was collected aseptically in a sterile bottom-hole sampler from a depth of 7,000 feet, under the personal supervision of a bacteriologist. Nothing had been introduced in the well for about 15 months prior to collecting the sample. While the hydrogen-producing bacteria found in the sample may have been introduced during or after the drilling of the well, the presence of such bacteria is indicative of the widespread distribution of hydrogen producers. Their presence, however, is not necessarily indicative of their activity in source sediments, particularly since most hydrogen producers are anaerobic spore formers which could be expected to survive almost indefinitely under favorable conditions.

TABLE III

DESCRIPTION OF RESERVOIR FLUIDS, 10 CC. SAMPLES OF WHICH CONTAINED BACTERIA WHICH FERMENTED EITHER GLYCEROL, GLUCOSE, OR CELLULOSE WITH FORMATION OF HYDROGEN, METHANE, AND CARBON DIOXIDE

Sample No.	*Location of Oil Well from Which Samples Were Taken*
XXIX: 61	Well No. 3, Apex Oil Company, El Segundo, Calif.
XXIX: 64-9	Coit Lease, Well C-95, Kendall Oil Co., Bradford, Pa.
XXIX: 65-12	Bingham 532, South Penn Oil Co., Bradford, Pa.
XXIX: 66-23	Cornen Lease, Well 11, Brundred Oil Co., Oil City, Pa.
XXIX: 67-30	Curtis Lease, Well 211, Moore Producing Co., Bolivar, N. Y.
XXIX: 93-7	Nitey No. 2, Amerada Petroleum Corp., Seminole County, Okla.
XXIX: 94-13	Zimmerman No. 1, Amerada Petroleum Corp., Lincoln County, Okla.
XXIX: 96-2	Sellers Lease, Well 2, Amerada Petroleum Corp., Des Allemands, La.
XXIX: 98-5	South Coast Lease, Well 8, Amerada Petrol. Corp., Lafourche, La.
XXIX: 102-10	Weil Lease, Well 6, Amerada Petrol. Corp., Cheneyville, La.
XXIX: 127-5	Kern Front, Well 15, General Petrol. Corp., Bakersfield, Calif.
XXIX: 138-1	Well 343-3P, Standard Oil Co., Kettleman Hills field, Calif.
XXIX: 141-2	Well 61K, Tide Water Associated Oil Co., Buena Vista, Calif.
XXIX: 146-4	Erburn No. 10, General Petroleum Corp., Capitan field, Calif.

Hydrogen production in mud samples.—It was proved that at least a little free hydrogen may be evolved by bacteria occurring naturally in samples of marine sediments to which nothing except sea water was added. Kilogram samples of organic-rich mud taken from the sea floor were mixed and covered with sea water in closed receptacles with connections for collecting evolved gases. Data from a representative experiment are summarized in Table IV. In this experiment 1250 grams of mud having an organic content of 3.8 per cent (wet basis) was incubated for several months at 27°C. Within a few days gas started to accumulate, which was found to contain hydrogen, carbon dioxide, and methane. The hydrogen and carbon dioxide content of the evolved gases decreased progressively and the methane content increased proportionately from month to month.

The stinking gases which escape from cores of certain sapropelic marine muds, upon being hauled to the surface from oceanic basins, have been observed to ignite with a plink resembling that of exploding hydrogen in the presence of a lighted match. When analyzed in the laboratory samples of such gases have been found to contain from 0.1–0.5 per cent hydrogen by volume. There is generally no free hydrogen in marine mud gases, although it occurs in certain sapropelic muds.

Allgeier *et al.* (3) observed the presence of 1–3 per cent hydrogen in the gases evolved during the fermentation of bottom deposits from Lake Mendota, which were studied under laboratory conditions. Gas was produced much more rapidly at 55°C. than at lower temperatures. The percentage of carbon dioxide and hydrogen increased and the percentage of methane decreased with a rise in temperature. A direct correlation was found between the numbers of bacteria and the quantity of gas produced (3).

Abundance of hydrogen producers in bottom deposits.—Most, but not all, one-gram samples of marine bottom deposits were found to contain bacteria which fermented either glycerol, peptone, or cellulose with the liberation of hydrogen. Methane producers were present in all such cultures. Intermittently heating the material to 80°C. for ten minutes could not be depended on to destroy selectively methane producers, because some of the latter survive such treatment. On the other hand, many or all of the hydrogen producers may be killed by such treatment. It should be apparent from the bacterial species named in Table I that by no means are all hydrogen producers thermotolerant. Schnellen (141a) has recently described a thermophilic methane-producing bacterium, *Methanosarcina barkerii*, which forms highly thermoresistant spores.

By employing the minimum dilution method, in which quantities of mud decreasing by powers of 10 were used as inocula, that is, 1.0 gram, 0.1 gram, 0.01 gram, *et cetera*, it was demonstrated that bottom deposits collected from the floor of the ocean contained up to 10,000 hydrogen-producing bacteria per gram and generally fewer than 1,000 methane producers per gram. This may be compared with counts of 31,000,000 aerobes, (probably facultative aerobes), 2,600,000 total anaerobes, 10,000 sulphate reducers, and 1,000 cellulose decomposers per gram of similar marine mud studied by ZoBell (191).

Hydrogen producers and methane producers, like the total bacterial population (193, 199), decrease in abundance with core depth, but such bacteria have been demonstrated in the bottom of cores 12–15 feet long. Whether such bacteria occur at greater depths can be determined only by the aseptic collection and careful examination of appropriate samples.

FACTORS WHICH INFLUENCE HYDROGEN PRODUCTION

Microbial flora.—The amount of hydrogen liberated by bacterial cultures depends to a large extent on the species present. Pure cultures of hydrogen producers (of which there are many known species) produce gas consisting of as much as 40–50 per cent hydrogen by volume. Little or no hydrogen may be liberated by mixed cultures.

Hydrogen producers may be overgrown in mixed cultures by other types of bacteria, or hydrogen may be utilized by other types of bacteria before it can escape from the medium. The elimination of hydrogen-utilizing bacteria by selective culture techniques often results in the formation of a gas much richer in hydrogen than gas produced by mixed cultures. This may be illustrated by an experiment with a sample of mud similar to that reported in Table IV, in which mixed microflora produced gas containing only 0.2–3 per cent hydrogen. By successively incubating freshly collected mud samples for 2 days at 27°C. and then heating to 80°C. for 20 minutes five different times to provide for the selective germination and destruction of methane-producing bacteria (which consume hydrogen), the subsequent incubation of the heat-treated mud resulted in the formation of gas which at first contained 40–50 per cent hydrogen, 40–55 per cent carbon dioxide, and only 5–10 per cent methane. Within 3 weeks, however, the methane producers had gained the ascendancy so that the evolved gas contained 70–80 per cent methane and less than 1.0 per cent hydrogen.

TABLE IV

TOTAL QUANTITY AND COMPOSITION OF GAS PRODUCED FROM 1,250 GRAMS OF MARINE MUD, CONTAINING 3.8 PER CENT OF ORGANIC MATTER (WET BASIS), AFTER DIFFERENT PERIODS OF INCUBATION AT 27°C. (ADAPTED FROM SENN, 143)

Incubation Period (Days)	*Total Gas Produced (Cubic Centimeters)*	*Percentage Composition of Gas*		
		CO_2	CH_4	H_2
0 to 22	80	25.9	71.1	3.0
23 to 29	260	23.9	73.5	2.6
30 to 43	460	23.7	74.3	2.0
44 to 57	570	21.7	77.0	1.3
58 to 65	700	21.5	77.3	1.2
66 to 72	980	20.8	77.8	1.4
73 to 97	1,490	20.8	78.0	1.2
98 to 179	2,430	21.2	78.3	0.5
180 to 289	3,260	19.0	80.4	0.6
290 to 431	3,660	18.7	80.3	1.0
432 to 575	4,100	16.6	83.2	0.2

The relative quantity of hydrogen produced by pure cultures varies within wide limits, depending on the substrate and experimental conditions. According to Grimbert (65), the gas produced by *Bacillus orthobutylicus* during the fermentation of glucose had the following composition after different periods of incubation:

	Percentage	
	Hydrogen	Carbon Dioxide
1st to 4th day	54	46
5th to 13th day	26	74
14th to 22nd day	22	78

The first portions of gas produced by several different bacterial species studied by Bennett and Pammel (20) consisted of almost pure hydrogen. The proportion of hydrogen decreased progressively and the carbon dioxide content increased with prolonged incubation. This was attributed (20) to the absorption by the medium of carbon dioxide, but several factors which influence the activity of the hydrogen-producing bacteria are now known to be involved.

Bacteria are not the only microörganisms which produce hydrogen. Species of *Scenedesmus* and other unicellular algae studied by Gaffron and Rubin (59) liberated hydrogen in the dark when the air was replaced by nitrogen. Certain algae were observed by Gaffron (58) to contain an enzyme, hydrogenase, which catalyzed a reversible reaction (either the production or utilization of hydrogen). The direction of the reaction depended on the concentration of reactants and environmental conditions.

Specific enzymes.—Hydrogenase is an enzyme produced by several microbial species. It catalyzes reactions in which molecular hydrogen reduces oxygen, methylene blue, fumarate, malate, formaldehyde, methyl alcohol, carbon monoxide, carbon dioxide, bicarbonate, nitrate, nitrite, sulphate, sulphite, thiosulphate, and other compounds (45, 79, 103, 157, 158). In the presence of such compounds, hydrogenase may cause the disappearance of molecular hydrogen from a system, although under certain conditions hydrogenase may activate the reverse reaction, that is, the liberation of molecular hydrogen. Hydrogenase has been shown to be an iron porphyrin-protein complex which is active only in the reduced or ferrous state (79, 103). The hydrogenase of luminous bacteria is inactivated by the presence of much oxygen (32) as is the hydrogenase of *Acetobacter peroxydans* (182).

Hydrogenlyase is the microbial enzyme most commonly responsible for the liberation of molecular hydrogen from organic compounds. It was established by the work of Stephenson and Stickland (159) that formic hydrogenlyase, which catalyzes the formation of hydrogen and carbon dioxide from formic acid, is a distinct enzyme and not the same as hydrogenase. The specificity of formic hydrogenlyase has been confirmed by the work of Woods (186).

Hydrogen is formed from formic acid by numerous bacteria (68, 83, 92, 128, 133, 167), and many bacteria which ferment organic compounds with the formation of hydrogen also produce formic acid (53–56, 68, 127). This suggests that microörganisms liberate hydrogen from organic compounds by producing formic acid and formic hydrogenlyase. However, Stephenson (156) has shown that molecular hydrogen is also produced by some other mechanism which does not involve formic hydrogenlyase. For example, Woods and Clifton (188) found that *Clostridium tetanomorphum* produced hydrogen from glucose, glycerol, pyruvate, and certain amino acids but not from formic acid, which definitely rules out the possibility of formic acid being an intermediary in hydrogen production by this organism.

Effect of temperature.—Mixed cultures of bacteria have been observed to produce hydrogen at temperatures ranging from 0° to 65°C. (29, 171). The optimum temperature for many pure cultures ranges from 25° to 45°C., although thermophilic hydrogen producers having higher optima are common. Mixed cultures of cellulose fermenters were found by Coolhaas (37) and Kroulik (100) to produce hydrogen more rapidly at 60°C. than at lower temperatures. Hydrogen was rapidly produced at 55°–60°C. by *Clostridium thermosaccharolyticum* during the fermentation of glucose (147). *Clostridium thermocellum* fermented cellulose with hydrogen formation at 62°–66°C. (171).

Spore-forming hydrogen producers have been demonstrated in marine bottom deposits, some of which were not killed by being heated for thirty minutes to 100°C. Advantage has been taken of the heat tolerance of such hydrogen producers to separate them from less tolerant contaminating organisms (111, 121, 122).

Nutrient requirements.—Sea water contains all of the mineral salts required for the physiological activity of marine hydrogen producers. Fresh-water strains grew in sea water diluted with 9 volumes of distilled water. Halophilic strains were encountered in oil-well or salt-lake brines which developed in homologous brine medium or in sea-water medium rendered isotonic with the brine by the addition of sodium chloride. Hydrogen production by bacteria growing in nutrient medium containing 30 per cent salt has been observed.

Ammonium satisfied the nitrogen requirements of most hydrogen producers. Their energy or carbon requirements are satisfied by fatty acids, amino acids, peptones, sugars, starches, cellulose, alcohols, glucosides, or other organic compounds. Some compounds shown to be fermented by various pure cultures with hydrogen formation are summarized in Table I. Although this survey of the literature is far from complete, it should be apparent from the fragmentary summary in Table I that a large variety of compounds, which one might expect to find in recent marine sediments, are fermented by bacteria with the formation of hydrogen.

A mixed culture of anaerobes from a sample of marine mud (XXX: 192F)
from nethane producers had been excluded by selective heat treatment was
ent numerous compounds with the formation of hydrogen. Repre-
are presented in Table V. In giving the volume and percentage
the evolved gases, corrections have been made for the amount of
nd hydrogen dissolved in the culture medium at the observed pH
Carbon monoxide was not found in any of the experiments.
pounds reported in Table V, cellulose, dextrin, inulin, peptone,
found to be fermented by mixed cultures of marine anaerobes

TABLE V

VOLUME AND PERCENTAGE COMPOSITION OF GAS PRODUCED DURING THE FERMENTATION OF 0.1 PER CENT OF VARIOUS COMPOUNDS BY ENRICHMENT CULTURE OF MIXED MICROFLORA FROM MARINE MUD XXX: 192F IN 160 CC. OF SEA-WATER MEDIUM INCUBATED AT 27°C. (ADAPTED FROM SENN, 143)

Compound	*Period of Incubation (Days)*	*Volume of Gas (Cubic Centimeters)*	*Percentage Composition of Gas*		
			CO_2	CH_4	H_2
Glycerol	27	68	52.4	0	47.6
Glucose	26	47	48.1	0	51.9
Lactose	25	22	59.8	0	40.2
Maltose	26	37	50.2	0	49.8
Sucrose	26	57	66.7	0	33.3
Starch	25	32	63.0	0	37.0
Sorbitol	27	33	54.4	0	45.6
Dulcitol	29	29	58.3	0	41.7
Mannitol	29	46	55.7	0	44.3
Levulose	30	40	48.6	0	51.4
Cellobiose	30	28	60.2	0	39.8
Raffinose	30	26	58.9	0	41.1
Glycogen	30	22	68.1	0	31.9
Salicin	30	24	56.3	0	43.7

with the formation of hydrogen (143). Monoacetin, diacetin, triacetin, and the following organic acids promoted hydrogen production in combination with glycerol: formic, acetic, propionic, butyric, caproic, stearic, lactic, pyruvic, succinic, maleic, malonic, tartaric, citric, and gluconic. Though only slowly attacked by anaerobes, both chitin and lignin appeared to promote hydrogen production by bacteria growing in sea-water medium enriched with glycerol. There was no evidence for hydrogen production from paraffine oil, although a little was produced from various samples of crude oil.

Effect of pH.—Hydrogen production by marine bacteria has been observed in nutrient media having initial pH values ranging from 5.5 to 9.8. The composition of the gas did not appear to be influenced by the hydrogen-ion concentration, but the rate of gas production was greatest between pH 7.0 and 8.3 (see data in Table VI). The pH of the marine bottom deposits studied by ZoBell (195) ranged from 6.4 to 9.5, most of them falling in the range of pH 7.5 to 9.0.

Hydrogen liberation is ordinarily accompanied by a decrease of the pH in experimental media, probably because organic acids are produced and weakly dissociated organic acids may be converted into more strongly dissociated ones. According to Buswell (29), glucose was gasified with the production of formic, acetic, propionic, butyric, and lactic acids. Formic acid and acetic acid were formed during the fermentation of propionic acid. Malic acid was fermented with the formation of propionic acid. Isobutyric acid was converted into lower fatty acids (29). Of course, the quantitative conversion of fatty acids to carbon dioxide, hydrogen, and methane could be expected to result in an increase in pH, and this actually happens after prolonged incubation.

Oxygen tension and redox potential.—The microbial production of hydrogen seems to be strictly an anaerobic process. Hydrogen is not liberated unless free oxygen is excluded from the medium. This may be because the hydrogen released by hydrogenlyases combines immediately with free oxygen to form water or it may be because hydrogenlyases are inactivated by free oxygen as are certain hydrogenases. According to Hoberman and Rittenberg (79), the hydrogenases and hydrogenlyases produced by *Proteus vulgaris*, *Escherichia coli*, and *Bacillus acidi lactici* are active only in the reduced state. Lascelles and Still (103) have found the hydrogenase of *E. coli* to be extremely sensitive to oxygen.

Not only should oxygen be excluded, but in order to obtain maximum hydrogen production the redox potential of the medium should be reduced to E_h −0.05 volt or lower. This can be achieved in most media by the addition of a little sodium sulphide or ascorbic acid. A redox potential of E_h −0.05 volt or lower is indicated by the reduction or decolorization of 0.002 per cent methylene blue added to the nutrient medium. As the growth of hydrogen producers progresses, the medium generally becomes more reducing, sometimes to the extent of E_h −0.45 volt. Hydrogen production by marine anaerobes has been found to be most rapid when the redox potential of the medium is between E_h −0.2 and −0.4 volt. The redox potential of most deep-sea sediments examined by ZoBell (195) ranged from E_h −0.05 to −0.35 volt, although the extreme values ranged from E_h +0.35 to −0.50. volt.

TABLE VI

GAS PRODUCED BY ENRICHMENT CULTURE OF ANAEROBES FROM MARINE MUD XXX: 192F DURING FERMENTATION OF GLYCEROL IN SEA-WATER MEDIUM HAVING DIFFERENT INITIAL pH VALUES. GAS VOLUMES ARE NOT CORRECTED FOR SOLUBILITY (ADAPTED FROM SENN, 143)

Initial pH of Medium	*First Gas after Number of Days*	*Volume of Gas after 44 Days (Cubic Centimeters)*	*pH after 44 Days*	*Percentage Composition of Gas*		
				CO_2	CH_4	H_2
5.55	44	1	5.70	—	—	—
6.30	12	123	5.70	39.1	0	60.9
6.45	12	134	5.70	35.9	0	64.1
7.00	5	161	5.85	38.9	0	61.1
7.45	7	167	5.85	39.8	0	60.2
7.90	7	159	5.95	37.1	0	62.9
8.35	8	163	6.00	35.8	0	64.2
8.85	19	134	6.10	39.6	0	60.4

OCCURRENCE OF MOLECULAR HYDROGEN IN NATURAL GASES

Marsh gas.—In spite of the rather widespread and abundant distribution in swamps, marshes, lake bottoms, and recent marine sediments of bacteria capable of fermenting a large variety of organic compounds with the formation of hydrogen, molecular hydrogen has only infrequently been demonstrated in gases emanating from swamps *et cetera*. Söhngen (150) attributed this general absence of hydrogen in such gases to the avidity of methane-producing bacteria for hydrogen in the presence of carbon dioxide:

$$CO_2 + 4H_2 = CH_4 + 2H_2O.$$

It is now known that sulphate reducers and other types of bacteria also utilize molecular hydrogen.

Söhngen (150) found that, although hydrogen is liberated from organic matter wherever the latter is undergoing fermentation in mud overlayered with water, molecular hydrogen generally is absent in marsh gas, fire damp, or gases evolving from bottom deposits. Söhngen's failure to find hydrogen in such gases was corroborated by similar observations by Bunsen, Graham, Playflower, Schloesing, Fouqué, Meyer, Oudemans, and other workers. From his review of the early literature Söhngen (150) was able to find only two isolated reports of hydrogen being found in gases emanating from bottom deposits: allegedly Hoppe-Seyler detected hydrogen in gases collected from Lake Constance, Switzerland, and Roozeboom demonstrated 0.2–6.4 per cent hydrogen in gases evolving from canal mud in Holland.

Popoff (133) was able to detect hydrogen in gases evolving from pond mud only rarely and then in small amounts. According to Harrison and Aiyer (73), hydrogen is usually absent in the gases of swamp rice soils. Only occasionally was a little hydrogen found (74). Harrison (72) declared that although both hydrogen and carbon dioxide may be generated in rice paddy soil, these two gases cannot exist in association under paddy soil conditions, because bacteria are present which activate the reduction of carbon dioxide to methane in the presence of molecular hydrogen. Harrison and Aiyer (72) believed that some of the hydrogen generated in rice paddy soils was reconverted into organic matter by bacteria near the surface of the soil.

A little dissolved hydrogen was found by Sugawara *et al.* (162) in the bottom waters of certain Japanese lakes which were rich in organic nutrients. Gas generated in fermenting, organic rich, bottom deposits from Lake Mendota was found by Allgeier *et al.* (3) to contain 1–3 per cent hydrogen, 3–30 per cent carbon dioxide, and 65–85 per cent methane. The extensive studies of Conger (36) on the ebullition of gases from Maryland marsh and lake waters revealed that hydrogen is either absent or present in only minute amounts. Some representative analyses of marsh gas were reported (36) as follows in terms of percentage by volume.

Gas	*Sample 1*	*Sample 2*	*Sample 3*	*Sample 4*
Carbon dioxide	2.4	1.5	1.8	2.3
Illuminants	0	0	0	0
Oxygen	0.2	1.2	0.3	0.3
Carbon monoxide	0	0	0	0
Hydrogen	0	0.5	0.2	0.2
Methane	72.2	82.2	57.8	61.7
Nitrogen	25.2	14.6	39.9	35.5

Based on an average gas production during the warm summer months of 26.27 cc. per square meter per hour, Conger (36) calculated that gas was produced in Maryland marshes at a rate of 90 cubic feet per acre per day.

Hydrogen in natural gas.—Brooks (26), Krejci-Graf (99), Lind (108), Pratt (135), and others (105) have commented on the notable absence of hydrogen in natural gas. However, a precursory examination of the literature reveals that hydrogen has been reported to be present in samples of natural gas from various parts of the world. Some of these reports are compiled in Table VII.

TABLE VII

SOME NATURAL GASES IN WHICH MOLECULAR HYDROGEN HAS BEEN REPORTED TO BE PRESENT

(These Data Should Be Viewed with Caution-C.E.Z.)

Location	*Field or Area*	*Percentage*				*Authority*
		CH_4	*CO_2*	*N_2*	*H_2*	
Indiana	Sullivan County	75.0	0	16.0	2.6	Bell (18)
Kansas	Dexter	15.0	0	84.0	0.8	Haworth and McFarland (76)
Michigan	Washtenaw County	69.0	0.6	3.6	26.0	Newcombe (115)
Michigan	Wayne County	67.9	0.7	3.5	25.6	Newcombe (115)
Ohio	Indiana	93.4	0.3	3.3	1.8	Croneis (39)
Ohio	Thurston	91.2	0.2	2.7	3.7	Croneis (39)
Rumania	Transylvania	99.0	0	0.2	0.4	Gardescu (61)
Russia	Koksher Island	79.2	0	0	20.8	Bodhanowicz (22)
Russia	Niznij-Tagile	9.5	0	20.7	66.5	Bohdanowicz (22)
Russia	Stavropol	37.5	0	21.1	27.3	Bohdanowicz (22)
S. Australia	Robe	39.6	1.3	30.7	25.4	Woolnough (189)

Lind (107) related that Rogers and Farr found 4–20 per cent hydrogen in 10 out of 82 samples of natural gas in New Zealand. Samples of natural gas from the petroleum region in the southern Urals were reported by Cherepennikov (31) to contain 4.6–12.7 per cent hydrogen. Hydrogen was said to be present in natural gas from the Melitopol and Melnikov fields, and 5.3–18.5 per cent hydrogen was reported to be present in gas from the Ssolikamsk lime deposits (31).

Data on the occurrence of hydrogen in natural gas must be interpreted with caution, since there are many sources of error in analytical and sampling procedures. For example, there is a possibility of hydrogen being formed in the well casing from the reaction of acidic waters on iron pipe:

$$Fe + H_2A = H_2 + FeA$$

where A is an acid radical. Hydrogen may also result from the reaction of hydrogen sulphide on iron (67, 131, 154):

$$Fe + H_2S = H_2 + FeS.$$

Other chemical or biological reactions may result in the generation of hydrogen in wells or in stored samples. On the other hand, the diffusibility of hydrogen and its reactivity with various chemical or biological agents may result in its rapid disappearance under certain conditions.

Hydrogen is known to occur in igneous rocks and volcanic gases (33, 116), from which it might infiltrate sedimentary deposits. The presence of 0.015 per cent hydrogen in Vesuvius gas from Agnana, Italy, 7.2 per cent hydrogen in fumarole gas from Kilauea, Hawaii, and 8.12 per cent hydrogen in fumarole gas from Mont Peleé, Martinique, has been reported by Dobbin (42).

On the other hand, hydrogen might occur in natural gas much more commonly than is indicated by the literature. Small quantities of hydrogen could easily be missed by many of the older analytical methods unless special efforts were made to detect it. Therefore, the mere fact that hydrogen is not reported as a constituent of natural gas does not necessarily mean that it is not present in at least minute amounts. While there are relatively few authentic accounts of the occurrence of hydrogen in natural gas, there are almost equally few conclusive accounts of its absence, although obviously hydrogen is rarely present in appreciable amounts.

Recently Brewer and Dibeler (25) of the National Bureau of Standards reported detecting by mass spectrometer analyses 0.36–0.70 mole per cent of hydrogen in helium gas from helium plants at Otis, Kansas, Exell, Texas, and Navajo, New Mexico. The presence of hydrogen was completely unsuspected, but confirmed by chemical tests. It was thought at first that the hydrogen might have come from the steel storage tanks, but helium from glass cylinders contained the same percentage of hydrogen ±0.01–0.03 mole per cent. An analysis of the natural gas showed that it contained a trace of hydrogen, the maximum being less than 0.05 mole per cent hydrogen, which was believed to be concentrated along with the helium in the purification process.

In response to queries, numerous personal communications have related the occurrence of small quantities of free hydrogen in natural gases associated with petroleum. In most cases, however, the data were from confidential files and their reliability was questioned for one reason or another. It is generally tacitly assumed, though, in routine analyses that natural gas contains no free hydrogen. Consequently, in the vast majority of cases no effect whatever has been made to detect hydrogen. Urgently needed in the quest for information on the origin of oil are reliable and extensive data on the occurrence or absence of free hydrogen in natural gases.

MICROBIAL UTILIZATION OF MOLECULAR HYDROGEN

Consumption of hydrogen in soil and sediments.—In 1839 de Saussure (41) observed the disappearance of hydrogen from soil. This was attributed to the oxidation of hydrogen to water, but it remained for Immerdorff (87) in 1892 to prove that hydrogen oxidation in soil is a biological process. Although moist soil caused the disappearance of hydrogen, heating the soil or treating it with chloroform or other antiseptics prevented hydrogen consumption. It has now been established that habituating soil and bottom deposits are several types of bacteria, both aerobic and anaerobic, which catalyze the oxidation of molecular hydrogen with the formation of water, methane, formic acid, formaldehyde, ammonia, hydrogen sulphide, and other products (8, 10, 94, 95, 149, 150, 157, 158, 160).

It has been observed by the U. S. Bureau of Mines (89) that when gases containing hydrogen are passed through soil, the gases lose part or all of their hydrogen. This was shown by Jones and Scott (89, 90) to be due to bacteria. Hydrogen was found to be oxidized by 24 samples of manhole sludge, two samples of anthracite mine waters, one sample of soil, and two samples of tap water. Hydrogen oxidation was more rapid when sponges were placed in the culture receptacles to increase the surface. Carbon monoxide consumers were also found in most of the samples. Hydrogen and carbon monoxide quantitatively disappeared in two to four weeks from gas mixtures containing originally 12–15 per cent hydrogen and 8–10 per cent carbon monoxide. In some tests methane was formed, but the consumption of oxygen indicated that most of the hydrogen and carbon monoxide was oxidized to water and carbon dioxide, respectively. Raw cultures of bacteria from sewage, sludge, soil, and water from coal mines caused the disappearance of hydrogen between pH 2.8 and 11.5 (91).

TABLE VIII

AMOUNT OF HYDROGEN CONSUMED BY BACTERIA AFTER DIFFERENT PERIODS OF TIME AT 27°C. IN 80 CC. OF SEA WATER ENRICHED WITH ORGANIC COMPOUNDS AND INOCULATED WITH ONE GRAM OF FRESHLY COLLECTED MARINE MUD

Bottle Number	*Substrate (0.1 Gram in 80 Cc.)*	*Hydrogen Uptake After 10 Days (Cubic Centimeters)*	*20 Days*
1	Benzoic acid, neopeptone	34	60
2	Phenol, neopeptone	32	55
3	p-Cresol, neopeptone	35	57
4	p-Hydroxybenzoic acid, neopeptone	27	47
5	p-Phenylethanol, neopeptone	37	56
6	Phenylalanine, tyrosine	30	61
7	Phenylalanine, tyrosine	37	—
8	Phenylalanine, tyrosine	32	58
9	Phenylalanine, tyrosine, neopeptone	52	—
10	None (sea-water control)	2	2

A rapid reduction of atmospheric pressure in closed receptacles filled with hydrogen and samples of marine mud has been observed. Gas analyses have shown that hydrogen was consumed. In one experiment, 20 grams of wet mud from Mission Bay was placed in each of three 180 cc. bottles containing 60 cc. of sea water and filled with hydrogen. After six weeks incubation at 27°C., analyses showed that 20.9, 37.6, and 65.2 cc. of hydrogen had been consumed in the three bottles, respectively, while none had disappeared from heat-sterilized controls, thereby indicating that bacteria or their enzymes in the mud were responsible for the consumption of hydrogen. In another experiment, the amounts of hydrogen reported in Table VIII were consumed by the bacteria in one gram of mud following its incubation for 10–20 days at 27°C. in 80 cc. of sea-water medium enriched with various organic substrates. Several samples of oil-well brines have similarly been found to contain bacteria which consumed hydrogen. Evidence for the utilization of molecular hydrogen by several types of bacteria, including both aerobic and anaerobic species, is reviewed in the following sections.

Oxidation of hydrogen by aerobic bacteria.—In 1906 Kaserer (94) isolated soil bacteria which were able to grow in a balanced mineral-salts medium in the presence of hydrogen, oxygen, and carbon dioxide. The bacteria oxidized hydrogen as a source of energy:

$$2H_2 + O_2 = 2H_2O.$$

Kaserer (95) described two species of hydrogen oxidizers, *Hydrogenomonas pantotropha* and *Carboxydomonas oligocarbophila*, both of which are probably widely distributed in soil and recent sediments. Haseman (75) found these two organisms in soil along with another unidentified species which oxidized hydrogen.

Further studies were made on the ability of autotrophic aerobes to assimilate hydrogen by Nabokich and Lebedeff (113), who observed in two representative experiments the consumption of the following quantities of gas.

Incubation Period	*Hydrogen*	*Oxygen*	*Carbon Dioxide*
(*Days*)	(*Cc.*)	(*Cc.*)	(*Cc.*)
18	100.6	42.9	14.0
15	187.1	95.4	14.6

Lebedeff (102) reported the isolation of a pure culture of a monotrichous, motile, rod-shaped bacterium called *Bacillus hydrogenes*, which could reduce nitrate in mineral medium in the presence of hydrogen and carbon dioxide. In the absence of carbon dioxide the reaction ceased. Suspended cells of *Bacillus hydrogenes* assimilated hydrogen and oxygen in the ratio of 2:1 in the absence of nitrate.

Niklewski (118) isolated *Hydrogenomonas flava* and *H. vitrea* from soil. Both organisms were found in canal mud, garden soil, pasture land, peat, and vegetable mold. They could grow either autotrophically utilizing hydrogen, carbon dioxide, and oxygen as the sole source of carbon and energy in mineral media, or they could grow heterotrophically in media enriched with organic compounds (119). *H. agilis* was also isolated and studied by Niklewski (120).

According to Ruhland (139), the ability of bacteria to assimilate molecular hydrogen as a source of energy is relatively widespread among bacteria. He isolated *Bacillus pycnoticus*, an aerobic autotroph, which has been described by Grohmann (66). Grohmann demonstrated in soil the presence of *Bacillus evanidus*, *B. lichenoides*, *B. retaneus*, *B. spurius*, and *B. suffuscus*, all of which oxidized hydrogen. Ruhland (140) found that the ratio of hydrogen oxidized to oxygen consumed by *B. pycnoticus* ranged from 2.14 to 2.78,the average H_2/O_2 ratio for several experiments being 2.56. A ratio of H_2/O_2 in excess of 2.0 is indicative of hydrogen being used to reduce carbon dioxide to formaldehyde (or similar product) in the synthesis of cell substance;

$$2H_2 + CO_2 = (HCHO) + H_2O.$$

B. pycnoticus consumed an average of one volume of carbon dioxide for each 6.8 volumes of hydrogen oxidized.

Tausz and Donath (170) noted that molecular hydrogen was oxidized by both *Bacterium aliphaticum liquefaciens*, which utilized paraffinic hydrocarbons ranging from pentane to decane, and by their "Methane bacterium," which utilized all straight-chain hydrocarbons tested, including methane. This and other observations suggest that the ability to utilize molecular hydrogen is rather common among hydrocarbon-oxidizing bacteria, of which more than a hundred species have been described (197).

A strain of *Acetobacter peroxydans* was found by Visser't Hooft (176) to be capable of utilizing hydrogen. Cultures were grown on agar plates in an atmosphere of two volumes of hydrogen to one of oxygen. The hydrogenase of this organism is inactivated by higher oxygen pressures (182). Lee and Umbreit (104) isolated from artificial cultures of legumes two species, *Hydrogenomonas pantotropha* and *Flavobacterium fucatum*, which oxidized hydrogen in the presence of oxygen and carbon dioxide. Both organisms appear to be widely and abundantly distributed in soil. Like other hydrogen oxidizers mentioned in this section, both organisms grew either autotrophically or heterotrophically in appropriate media. Kluyver and Manten (98) found that heterotrophically grown cells of *Hydrogenomonas flava* did not oxidize hydrogen, although autotrophically grown ones did. The latter were able to oxidize hydrogen either autotrophically or heterotrophically. The presence of lactate in suspensions of "resting" cells increased the rate of hydrogen uptake.

Escherichia coli was found by Lascelles and Still (103) to contain an enzyme, hydrogenase, which catalyzed the so-called "Knallgas" reaction, or the utilization of molecular hydrogen in the presence of oxygen. They confirmed the work of Hobermann and Rittenberg (79) that hydrogenase is an iron porphyrin-protein complex active only in the reduced or ferrous state. This is in agreement with the finding of Claren (32) and Wieland and Pistor (182) that hydrogenase is inactivated by the presence of much oxygen. Additional observations on the Knallgas reaction have been made by Yamagata and Nakamura (190).

Hydrogen utilization by methane producers.—Bacteria which ferment virtually all types of organic compounds with the formation of methane are found in abundance in soil, sewage, marine bottom deposits, lakes, rivers, canals, ponds, swamps, *et cetera* (3, 8, 29, 30, 36, 44, 72, 83, 143, 171, 196). As a rule, it is much easier to demonstrate the presence of methane producers than hydrogen producers. The inoculation of appropriate nutrient media with samples of such materials nearly always results in the production of methane, but it is often only with difficulty that hydrogen producers can be demonstrated. This has been attributed to the utilization of molecular hydrogen by methane-producing bacteria.

Many workers have observed an inverse relationship between the amount of methane and hydrogen in gases formed from materials undergoing fermentation by mixed microflora (29, 111, 121, 150). The highest percentage of hydrogen generally occurs in the first gas produced, after which the content of hydrogen and carbon dioxide decreases and the content of methane increases. After prolonged incubation of such mixed cultures no free hydrogen may be evolved, or added hydrogen may actually be consumed. This was first demonstrated in 1905 by Söhngen (149), who observed the dissipation of 1,191 cc. of hydrogen and 300 cc. of carbon dioxide by a formate culture from which he recovered 285 cc. of methane:

$$CO_2 + 4H_2 = CH_4 + 2H_2O.$$

The ratio of hydrogen consumed to methane produced was 4.18 and the H_2/CO_2 ratio was 3.97, both ratios closely approximating the theoretical value of 4.00. The H_2/CO_2 ratio in one of Buswell's (29) experiments in which pre-formed cells of methane bacteria consumed 3,415 cc. of carbon dioxide and 13,685 cc. of hydrogen with the production of 3,490 cc. of methane was 4.01.

In two other experiments Söhngen (150) observed the disappearance of 950 and 1,000 cc. of hydrogen under the influence of 50 cc. of medium containing a pure culture of a methane producer in 25 days at 35°C. He also observed the utilization of hydrogen by cultures during the fermentation of calcium butyrate and calcium formate with the formation of more methane than could be accounted for by the carbon in the butyrate or formate, thereby indicating that carbon dioxide from calcium bicarbonate (the only other source of carbon in the medium) was reduced to methane.

The observations of Söhngen were confirmed by Lieske and Hofmann (106) who showed further that carbon monoxide was also reduced by hydrogen to methane:

$$CO + 3H_2 = CH_4 + H_2O.$$

Using mixed cultures of bacteria, Fischer *et al.* (49) demonstrated the reduction of both carbon dioxide and carbon monoxide to methane by hydrogen.

Hydrogenase produced by methane bacteria was found by Stephenson and Stickland (160) to catalyze the combination of molecular hydrogen with not only carbon dioxide and carbon monoxide but also with formic acid, formaldehyde, and methyl alcohol to give methane:

$$HCOOH + 3H_2 = CH_4 + 2H_2O$$

$$HCHO + 2H_2 = CH_4 + H_2O$$

$$CH_3OH + H_2 = CH_4 + H_2O.$$

Neither acetic acid, propionic acid, butyric acid, caprylic acid, ethyl alcohol, acetaldehyde, nor glucose was reduced to methane by hydrogen in the presence of hydrogenase, thereby leading Stephenson and Stickland (160) to conclude that only compounds with one carbon atom are reduced directly to methane. Recent observations by Schnellen (141a) indicate that even one-carbon-atom compounds may be first fermented to carbon dioxide before being reduced to methane.

In the methane fermentation of ethyl alcohol by an enrichment culture obtained from sewer mud, Barker (8) found that the alcohol was dehydrogenated almost quantitatively to acetic acid and at the same time there was consumed a quantity of carbon dioxide equivalent to the methane formed. Similar results were obtained with butyl alcohol. Barker favored the view that methane production by bacteria is a plain reduction by hydrogen of carbon dioxide or other one-carbon-atom compounds resulting from the breakdown of larger molecules. Using washed cells of *Methanobacterium omelianskii*, Barker (10) noted the formation of methane from the uptake of 92.4 cmm. of carbon dioxide and 326.0 cmm. of hydrogen, a H_2/CO_2 ratio of 3.53 as compared with 4.0 for the theoretical reaction:

$$CO_2 + 4H_2 = CH_4 + 2H_2O.$$

The reaction was found to occur between pH 5.2 and 8.6 and was nearly independent of pH between 5.8 and 7.7. The carbon dioxide tension and the concentration of bicarbonate were influenced by the pH. The rate of hydrogen uptake and carbon dioxide reduction changed greatly with carbon dioxide concentration, the rate approaching a maximum at about 3×10^{-4} moles per liter of carbon dioxide.

In experiments with carbon dioxide containing radioactive carbon, C^{11}, Barker *et al.* (13) demonstrated quite conclusively that two species of methane-producing bacteria, *Methanobacterium omelianskii* and *Methanosarcina methanica*, reduced carbon dioxide to methane, by showing that the methane contained radioactive carbon. These experiments considerably strengthen the generalization that the methane fermentation of organic as well as inorganic compounds is essentially an anaerobic process in which carbon dioxide acts as the ultimate hydrogen acceptor and is reduced to methane. Some of the carbon dioxide was converted into bacterial cell substance (13).

The conversion of a mixture of carbon dioxide and hydrogen to methane by *Methanosarcina barkerii*, *Methanobacterium formicicum*, and *Methanobacterium omelianskii* has been reported by Schnellen (141a). Other one-carbon-atom compounds tested lacked the ability to replace carbon dioxide as a hydrogen acceptor, although *Ms. barkerii* fermented methyl alcohol and acetate and *Mb. formicicum* fermented formate with the formation of carbon dioxide, which could then be reduced to methane. The last two named organisms catalyzed the conversion of carbon monoxide into methane and carbon dioxide according to the equation:

$$4CO + 2H_2O = CH_4 + 3CO_2.$$

The reaction was catalyzed even in an atmosphere of pure carbon monoxide. Evidence is presented by Schnellen (141a) that the methane formed by *Ms. barkerii* in an atmosphere of carbon monoxide and hydrogen results partly from the fermentation of carbon monoxide, as in the foregoing reaction, and partly from the reduction of the carbon dioxide.

Reduction of CO_2 to carboxylic acids.—Harden's (68) observations in 1901 suggested that in the fermentation of glucose, *Escherichia coli* was able to catalyze the following reversible reaction resulting in the formation or degradation of formic acid:

$$CO_2 + H_2 = HCOOH.$$

An increase in the partial pressure of carbon dioxide appeared to cause the reaction to go to the right. Increasing the hydrostatic pressure by 0.5 atmosphere increased the yield of formic acid from three to ten times. These observations were confirmed by Woods (186), who showed that *E. coli* produced an enzyme, formic hydrogenlyase, which catalyzed the reduction of carbon dioxide to formic acid when the partial pressure of hydrogen was increased. Hydrogen uptake by the system seemed to require the presence of both carbon dioxide and bicarbonate, the latter probably because of its effect on the pH.

The formation of acetic acid by mixed cultures of methane bacteria was observed by Fischer *et al.* (50), who believed it to be formed from the reduction of carbon dioxide by hydrogen in much the same way as methane is formed. Wieringa (183) isolated from mud an anaerobic spore former, *Clostridium aceticum*, which was able to oxidize hydrogen with the reduction of carbon dioxide and the formation of acetic acid:

$$2CO_2 + 4H_2 = CH_3COOH + 2H_2O.$$

The reduction of carbon dioxide with the formation of acetic acid by *Clostridium thermoaceticum* was demonstrated by Barker and Kamen (11). Two molecules of acetic acid were believed to be condensed and reduced further by *Butyribacterium rettgeri* with the formation of butyric acid (12):

$$2CH_3COOH + 4H = CH_3CH_2CH_2COOH + 2H_2O.$$

All of the carbon atoms in the butyric acid were shown to be derived from carbon dioxide because the carboxyl, alpha, and beta carbon atoms were all radioactive, C^{14}, as was the carbon in the carbon dioxide from which the butyric acid was synthesized.

Fixation of CO_2 as microbial cell substance.—Many microörganisms have been observed to synthesize cell protoplasm from compounds formed by the reduction of carbon dioxide by molecular hydrogen. This is probably true of all of the autotrophic bacteria which oxidize hydrogen. Kaserer (94) believed that *Hydrogenomonas pantotropha* synthesized cell substance by reducing carbon dioxide to formaldehyde:

$$CO_2 + 2H_2 = (HCHO) + H_2O.$$

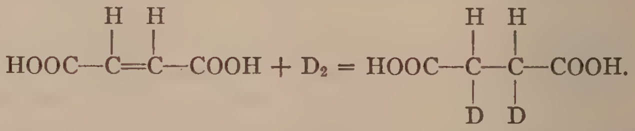
The formaldehyde might then be polymerized or condensed with the formation of more complex compounds. The consumption of carbon dioxide coupled with a ratio of H_2/O_2 consumed in excess of 2 and the accompanying development of cells of *Bacillus pycnoticus* in mineral-salts solution convinced Ruhland (140) that this autotrophic hydrogen oxidizer converted carbon dioxide into a carbohydrate-like compound. Under the most favorable conditions of growth *Bacillus pycnoticus* consumed 6.8 volumes of hydrogen for each volume of carbon dioxide changed to organic carbon.

Some, if not all, of the methane producers, which are strictly anaerobic, utilize carbon dioxide in the synthesis of cell material. This was proved to be true of *Methanosarcina methanica* and *Methanobacterium omelianskii*, which converted into cell substance from 5 to 10 per cent of the total carbon dioxide assimilated, according to estimates made by Barker *et al.* (13). *Methanosarcina barkerii*, which catalyzes the conversion of carbon dioxide and hydrogen into methane, used part of the gas mixture for building new cell material (141a).

Gaffron (58) found that algae of the family *Scenedesmus* could activate and utilize molecular hydrogen in connection with several metabolic processes, including the reduction of carbon dioxide and other metabolites in the synthesis of cell substance. Additional examples of the utilization of hydrogen by photosynthetic bacteria are cited by Gaffron (58).

Reduction of organic substances by hydrogen.—Reference has already been made to the reduction of one-carbon-atom compounds, including formic acid, formaldehyde, and methyl alcohol with the formation of methane (8, 141a, 160). The hydrogenase, produced by *Escherichia formica* and other bacteria, was shown by Stephenson and Stickland (157) to catalyze the reduction of fumarate and methylene blue by molecular hydrogen. The reduction of fumarate and methylene blue by *E. coli* at the expense of hydrogen was demonstrated by Lascelles and Still (103).

Farkas and Fischer (45) have investigated the hydrogenation of fumarate, maleate, malate, carbonate, and oxygen by *Proteus vulgaris*. The rate at which fumarate was reduced was directly proportional to the partial pressure of hydrogen but independent of the fumarate concentration above 1/80 molar. The hydrogenation of fumarate by heavy hydrogen (D_2) with the formation of isotopic succinate in the presence of *E. coli* has been studied by Farkas and Schneidermesser (46):



$$\mathrm{HOOC{-}\overset{H}{\overset{|}{C}}{=}\overset{H}{\overset{|}{C}}{-}COOH + D_2 = HOOC{-}\underset{\underset{D}{|}}{\overset{\overset{H}{|}}{C}}{-}\underset{\underset{D}{|}}{\overset{\overset{H}{|}}{C}}{-}COOH.}$$

The relative rates at which various amino acids and other compounds were hydrogenated with molecular hydrogen by suspensions of *Clostridium sporogenes* at pH 7.1, as reported by Hoogerheide and Kocholaty (82), are as follows, arranged in order of decreasing reducibility:

Hydroxylamine	100	Acrolein	47	Methionine	15
Proline	100	Diacetyl	40	Acetic acid	5
Glycine	100	Acetaldehyde	33	Glutaric acid	5
Ornithine	100	Glyceric aldehyde	26	Glyoxal	5
Arginine	80	Cysteine	22	Oxalic acid	4
Tryptophane	67	Tyrosine	20	Malonic acid	4
Acetylmethylcarbinol	50	Cystine	16	Aspartic acid	2

The amino acids were deaminized with the liberation of ammonia. Additional examples of the microbial reduction of organic substances with hydrogen are given by Claren (32) and Wieland and Pistor (182).

Reduction of nitrate by hydrogen.—Hydrogenase produced by *Escherichia formica* was shown by Stephenson and Stickland (157) to cause the reduction of nitrate in the presence of molecular hydrogen. Washed suspensions of two strains of *E. coli* studied by Woods (187) brought about the reduction of nitrate, nitrite, and hydroxylamine to ammonia in the presence of hydrogen:

$$HNO_3 + 4H_2 = HN_4OH + 2H_2O$$

$$HNO_2 + 3H_2 = NH_4OH + H_2O$$

$$NH_2OH + H_2 = NH_4OH.$$

Similar reactions were catalyzed by washed suspensions of *Clostridium welchii* (187). *Bacillus hydrogenes* Lebedeff (102) used hydrogen to reduce nitrate. Niklewski (120) claimed to have isolated an anaerobic organism, *Hydrogenomonas minor*, which reduced both nitrate and sulphate with molecular hydrogen, but no details were given.

The reduction of nitrate or nitrite, like the reduction of oxygen, probably plays no important part in the utilization of hydrogen in petroliferous sediments, because neither nitrate, nitrite, nor free oxygen is present. However, in recently deposited sediments and in the overlying water where these hydrogen acceptors are commonly present, they may contribute to the depletion of hydrogen, or viewed from another angle, hydrogen-oxidizing bacteria may contribute to the depletion of oxygen, nitrate, and nitrite.

Reduction of sulphate by hydrogen.—In 1907 Nikitinsky (117) demonstrated the presence of anaerobes in ditch water which utilized molecular hydrogen. It was suggested but not proved that hydrogen was oxidized at the expense of sulphate. In 1913 Kroulik (100) attributed the formation of hydrogen sulphide in a cellulose medium inoculated with hydrogen-producing anaerobes to the interaction of evolved hydrogen and sulphate. The following year Niklewski (120) reported that sulphate was reduced by hydrogen-oxidizing bacteria.

In 1931 Stephenson and Stickland (157) worked with an enrichment culture of anaerobes from river mud which synthesized methane from a mixture of carbon dioxide and hydrogen and simultaneously reduced sulphate to sulphide at the expense of molecular hydrogen. From this culture they (158) isolated a new species, designated Strain 182, washed suspensions of which reduced sulphate to hydrogen sulphide with the consumption of hydrogen:

$$H_2SO_4 + 4H_2 = H_2S + 4H_2O.$$

Strain 182 similarly reduced sulphite and thiosulphate to hydrogen sulphide.

A mixed culture of organisms in canal water was observed by von Wolzogen Kühr and van der Vlugt (177) to reduce sulphate while utilizing hydrogen. In one experiment 200 cc. of gaseous hydrogen trapped over one liter of canal water was entirely consumed in 3 weeks.

The ability of sulphate reducers to live autotrophically, obtaining energy from the oxidation of hydrogen and carbon from carbon dioxide or bicarbonate, was reported by Wight and Starkey (184). Such bacteria were believed by Starkey and Wight (154) to contribute to the anaerobic corrosion of metallic iron by utilizing the hydrogen which resulted from the reaction between iron and water:

$$Fe + 2H_2O = Fe(OH)_2 + H_2 \text{ (Anodic solution of iron)}$$

$$H_2SO_4 + 4H_2 = 4H_2O + H_2S \text{ (Depolarization).}$$

The depolarization product, hydrogen sulphide, contributes further to the corrosion of iron by combining with the anodic solution of ferrous iron:

$$Fe(OH)_2 + H_2S = FeS + 2H_2O.$$

Experimental evidence for the direct utilization of cathodic hydrogen on corroding iron has been reported by Menard and Berkalof (112), Pomeroy (131), and Pont (132). Pont observed the growth of sulphate-reducing bacteria in a mineral-salts medium containing steel wool and no source of energy other than the hydrogen resulting from the reaction of the steel wool with water. Carbon dioxide or bicarbonate was the only carbon source in the medium. Starkey and Wight (155) noted the reduction of sulphate in inorganic medium containing steel wool, which provided the hydrogen by reacting with water.

In a medium containing lactate, sulphate reducers were observed by Starkey and Wight (155) to reduce more sulphate to hydrogen sulphide than could be accounted for by the quantity of lactate present. In 100 cc. of inorganic medium, sulphate reducers consumed 85–211 cc. of hydrogen in about 8 weeks at 28°C. while reducing sulphate to hydrogen sulphide. The carbon requirements of sulphate reducers, which grow in mineral medium and oxidize hydrogen, were satisfied by bicarbonate or carbon dioxide. Growth occurred only in strictly anaerobic media, the optimum redox potential ranging from E_h -0.2 to -0.3 volt. Growth occurred between pH 5.5 and 8.5.

Sulphate reducers isolated from recent marine sediments have been shown to consume hydrogen. In one series of experiments pure or partially purified cultures of sulphate reducers were planted in sea-water medium enriched with 0.02 per cent each of calcium lactate, ascorbic acid, and ferrous ammonium phosphate, and 0.5 per cent potassium sulphate and a like amount of sodium bicarbonate. After 2 weeks' incubation, during which period most of the lactate was utilized and a good crop of bacteria was produced, sterile 180-cc. bottles were filled to capacity in duplicate with the seeded medium. Then all but 20 cc. of the medium was replaced with hydrogen. Each culture bottle was fitted with a mercury manometer to provide for following changes in the gas tension and with connections to provide for collecting the gas for analysis at the conclusion of the experiment.

Controls indicated that a little hydrogen was lost through leakage, diffusion, or other experimental errors, but the amount lost was relatively small as compared with the amount that disappeared in the presence of sulphate-reducing bacteria. The amounts of gas consumed by different cultures in 6 weeks at 28°C. are given in Table IX. Total sulphides in the cultures were determined and calculated as hydrogen sulphide.

TABLE IX

HYDROGEN CONSUMED AND HYDROGEN SULPHIDE PRODUCED IN 6 WEEKS AT 28°C. BY PURE OR PARTIALLY PURIFIED CULTURES OF SULPHATE REDUCERS IN 20 CC. OF SEA-WATER MEDIUM ENRICHED WITH 0.02% CALCIUM LACTATE, 0.02% ASCORBIC ACID, 0.02% $FeNH_4PO_4$, 0.05% SODIUM BICARBONATE, AND 0.5% POTASSIUM SULPHATE

Culture No.	*Source of Cultures*	*H_2 Consumed (Cc.)*	*H_2S Produced (Cc.)*	*Ratio H_2/H_2S*
XXIV: 39-1	Mud from Mission Bay	58	13	4.5
XXIV: 39-2	San Diego Bay mud	41	8	5.1
XXIV: 39-3	Sorrento Slough mud	43	9	4.8
XXIV: 39-5	Deep sea mud	20	4	5.0
XXIV: 39-7	Marine mud core	55	12	4.6
XXIV: 39-8	Marine mud core	53	10	5.3

In each case the ratio of hydrogen consumed to hydrogen sulphide produced exceeded the theoretical value of 4.0 which would result if hydrogen were oxidized quantitatively to hydrogen sulphide and water. This suggests that part of the hydrogen was used in other ways than the reduction of sulphate. Part of the hydrogen may have been used to reduce carbon dioxide in the synthesis of cell substance. Incidentally, the amount of hydrogen sulphide from sulphate reduction that could result from the quantitative utilization of the lactate and ascorbic acid would be less than 1 cc. in the 20 cc. of culture medium.

In similar experiments with a larger volume of culture medium and a smaller volume of gas, it was found that sulphate reducers caused the quantitative disappearance of hydrogen.

DISCUSSION

Fate of hydrogen in sediments.—The demonstrated ability of sulphate reducers to utilize molecular hydrogen suggests that such bacteria may be instrumental in preventing the accumulation of hydrogen resulting from the fermentation of organic matter (29, 143), radioactivity (19, 23, 80, 81, 110, 144, 145, 172), or from various chemical reactions in the earth's crust (116). Sulphate reducers appear to occur in abundance in recent marine sediments (191, 196), and they have been found in oil-well brines from various depths (14, 15, 60, 62, 63, 198). Of course, it is a moot question whether bacteria found in samples of reservoir fluids are indigenous species or if they are adventitious species introduced during drilling or production practices. However, the continued abundance of bacteria in produced fluids for prolonged periods after anything has been introduced into the oil wells, the peculiar types of organisms found, evidence that sulphate has been reduced to hydrogen sulphide, and the demonstrated ability of sulphate reducers to function under similar environmental conditions all speak for the occurrence and activity of bacteria in certain petroleum deposits.

Assuming that sulphate reducers or their enzymes have been active in source sediments of petroleum, each gram of hydrogen sulphide derived from sulphate could account for the utilization of no less than 2,600 cc. of hydrogen:

$$H_2SO_4 + 4H_2 = H_2S + 4H_2O.$$

If the sulphate reducers developed autotrophically, as they are known to do under certain conditions (132, 155, 184), more than 700 cc. of hydrogen would disappear for each gram of hydrogen sulphide derived from the reduction of sulphate in this way. A large variety of organic compounds as well as certain petroleum hydrocarbons (169, 197, 198) are utilized as energy sources by sulphate reducers, but thermodynamically hydrogen would be the best source of energy for sulphate reduction, provided the necessary catalysts or enzymes were present.

Competing for hydrogen in sediments might be methane-producing bacteria. The evidence (8, 10, 13, 29, 49, 106, 141a, 150, 160) seems to be conclusive that most, if not all, biologically produced methane results from the reduction of carbon dioxide or other one-carbon-atom compounds by hydrogen:

$$CO_2 + 4H_2 = CH_4 + 2H_2O.$$

There is very little information on the occurrence of methane-producing bacteria in oil-bearing formations, but such bacteria are common inhabitants of recent sediments (3, 29, 30, 36, 44, 72, 196). Many methane producers are anaerobic, salt-tolerant thermophiles, which grow at temperatures at least as high as 65°C. and possibly higher. Methane producers have been found in oil sands (62) and in several samples of oil-well brines (198), although it is still uncertain whether these bacteria are indigenous or adventitious species. Nevertheless, the possibilities that such bacteria have been active in source sediments of petroleum command attention. Even if living methane producers cannot be demonstrated, the possible effects of "resting" or pre-formed cells (10, 29) or their enzymes (160) should be carefully considered.

Assuming that methane producers or their enzymes have been active in source sediments of petroleum, each cubic centimeter of methane produced by this mechanism could account for the disappearance of at least 4 cc. of hydrogen; more if the methane producers fixed hydrogen in the synthesis of cell substance as some are known to do (13).

Also of geological importance is the reduction of bicarbonate or carbon dioxide by methane producers and other types of bacteria, because this could help explain the porosity of limestone. In the presence of water, carbonate dissociates to give bicarbonate and/or carbon dioxide, depending primarily on the pH:

$$CO_3^{--} \rightarrow HCO_3^{-} \rightarrow CO_2.$$

The consumption of carbon dioxide or bicarbonate would cause the reaction to proceed to the right. On the assumption that methane producers have done this, each cubic centimeter of methane thus formed could account for the disappearance of 4.27 milligrams of calcium carbonate.

Also contributing to the dissolution of carbonates might be bacteria which reduce carbon dioxide to formic (68, 186), acetic (11, 50, 183), butyric (11), or other carboxylic acids (181). The production of formic acid has been shown to be reversible, an increase in the partial pressure of the gases causing the following reaction to go to the right (68, 186):

$$CO_2 + H_2 = HCOOH.$$

Organic acids produced by such a mechanism would not only fix carbon dioxide, but the acid itself would tend to convert carbonate into carbon dioxide:

$$CaCO_3 + 2HA = CaA_2 + CO_2$$

where A is an acid radical. Of course, it is highly problematical whether such bacteria have been active in source beds of petroleum, but the possibilities indicate the desirability of exhaustive research work to determine all of the facts.

Besides utilizing hydrogen for methane production, sulphate reduction, and the formation of organic acids, bacteria may activate the hydrogenation of organic compounds, thereby forming compounds which are more petroleum-like. The microbial reduction of fumarate (45, 46, 103, 157), amino acids (82), unsaturated fatty acids (198), and other organic compounds (31, 43, 82, 182) by molecular hydrogen has been reported. The competition for hydrogen by methane formers, sulphate reducers, and other types of bacteria which fix hydrogen might explain the exiguity or lack of hydrogen in source beds of petroleum and at the same time help to account for the origin of oil.

Microbial production of hydrogen in sediments.—The literature and data summarized hereinbefore indicate that sedimentary materials harbor numerous species of bacteria capable of fermenting a large variety of organic compounds with the formation of hydrogen.

Experiments with enrichment cultures of hydrogen producers indicate that 40–50 cc. of hydrogen may be liberated for each gram of organic matter in marine sapropel that is fermented. As much as 80 cc. of hydrogen may be liberated from the fermentation of one gram of carbohydrate (29).

Hydrogen-producing bacteria are believed to be active in recent organic sediments, where the affinity of other reactants for hydrogen prevents its accumulation. The depth to which hydrogen-producing bacteria are active in older sediments is probably limited primarily by the amount of utilizable organic matter present. Finding hydrogen-producing bacteria in oil-well brines (198) and oil sands (62) is significant. Much more work will have to be done on the occurrence of utilizable organic matter and hydrogen-producing bacteria in petroliferous sediments before the role of such bacteria in the origin of oil can be appraised, although available information indicates that such bacteria may play an important role, particularly in the early stages of the decomposition of organic matter.

Porfiriev (134) has expressed the view that the bacterial fermentation of organic matter is the source of hydrogen for the hydrogenation reactions which result in the formation of oil. Pratt (135) contended that the natural evolution of oil consists essentially of a hydrogenation or methylation process, but he deplored a lack of the requisite hydrogen. The catalytic hydrogenation theory of oil formation is also questioned by Brooks (26) owing to the lack of hydrogen in natural gas.

Amicrobial generation of hydrogen.—Nichols (116) has summarized several chemical reactions which may account for the formation of free hydrogen in the earth's crust when conditions are right. Most of these reactions require rather high temperatures, so if they occur at all, most likely it would not be in environments where petroleum occurs. However, it is conceivable that some hydrogen may be formed at great depths in the earth's crust and diffuse toward the surface. In this latter category is hydrogen that may result from the action of superheated steam on carbon in the presence of an appropriate catalyst:

$$C + 2H_2O = 2H_2 + CO_2.$$

This reaction is rather highly endothermal and a continual supply of energy must be provided or the reaction will cease shortly. Superheat in steam is not sufficient; the carbon must be at the point of incandescence.

Another possibility is the reaction of superheated steam with ferrous oxide:

$$3FeO + H_2O = H_2 + Fe_3O_4.$$

It should be pointed out that the higher oxides of iron are very rarely found below the water table, so if the above reaction takes place, it would be under exceptional rather than general conditions.

It has been postulated that ferrous sulphide may react with hydrogen sulphide to yield hydrogen:

$$FeS + H_2S = FeS_2 + H_2.$$

It is yet to be established that this reaction will take place under conditions found within the "geological fence" (38a), although Heck (77) has presented an interesting argument that the reaction between ferrous sulphide and hydrogen sulphide may provide hydrogen for the hydrogenation of organic matter in the genesis of petroleum. He stated that oil-bearing sediments generally contain FeS_2 and not FeS, although FeS is formed by the reaction of ferrous iron with hydrogen sulphide from reduced sulphate.

According to data summarized by Clarke (33), free hydrogen has long been known to be present, even in high concentrations, in the gases from many volcanoes. It is almost universally present in igneous rocks, and the older igneous rocks show higher concentration of molecular hydrogen than the geologically younger igneous rocks. On a basis of many analyses, it has been estimated that one cubic kilometer of granite would yield 5,293,000,000 cubic meters of hydrogen (at normal temperature and pressure). One 100-gram sample of granite yielded 134.61 cc. of free hydrogen (33). This hydrogen may result from chemical reactions or from the radioactivation of compounds containing hydrogen.

Radioactivity may be an important source of hydrogen in earth formations. The work of Lind and Bardwell (110) and Honig and Sheppard (81) has shown that the alpha-particle bombardment of gaseous hydrocarbons results in the liberation of appreciable quantities of hydrogen. The formation of hydrocarbons and much hydrogen from the alpha radiation of organic acids has also been reported (23, 80, 145, 146). These observations are very significant in view of the distribution of radioactivity in petroliferous sediments (16, 17, 19, 144) and the rather common occurrence in natural gases of helium (42, 47, 48, 105), a by-product of radioactivity.

Lind (107, 108) advanced a theory to account for the formation of paraffinic, and possibly other, hydrocarbons from the polymerization and condensation of lower members of the series under the influence of radioactivity. The theory has been championed and amplified by A.P.I. Research Project 43C workers (16, 17, 19, 23, 80, 81, 144, 145, 146). The theory that radioactivity has contributed to the origin of oil seems plausible, except for the objection that alpha radiation causes the liberation of hydrogen from all compounds containing hydrogen which have been bombarded, and hydrogen is generally absent in oil-bearing formations. This objection should be reconsidered in view of the ready utilization of hydrogen by methane-producing, sulphate-reducing, carbon dioxide-fixing, and other types of bacteria. Moreover, as has already been pointed out, hydrogen is actually sometimes present in natural gas associated with petroleum.

Radioactivity may activate the combination of hydrogen with various compounds. Alpha particles from radon in mixtures of carbon monoxide and hydrogen resulted in the formation of formaldehyde, water, and mostly methane, according to Scheuer (141). Lind and Bardwell (109) were unable to confirm this observation, but they did show that the alpha-particle bombardment of a 1:1 mixture of carbon monoxide and hydrogen resulted in the disappearance of the reactants with the formation of carbon dioxide and a white, non-crystalline, paraffine-like solid. The alpha-particle bombardment of a 1:2 mixture of carbon dioxide and hydrogen yielded water plus an unidentified addition product of the two reactants, but no methane (109).

Some thermodynamic considerations.—The free energy of reaction, conventionally expressed as a ΔF value, is a factor which determines whether a given reversible reaction may take place spontaneously in the presence of appropriate catalysts and concentrations (activities). A negative ΔF indicates that the tendency will be for the reaction to go to the right, a positive ΔF indicates that the tendency will be for the reaction to go to the left. It would require the application of work, electrical energy, or some other form of free energy from outside sources to make a reaction having a positive ΔF proceed to the right.

The ΔF values for the following reactions have been calculated from the free energies of formation of gram-molar quantities of reactants at the standard state (6), namely, 1 mole per 1,000 grams of solvent, 1 atmosphere of gas pressure, and 25°C. The ΔF values are influenced by the temperature, concentrations (activities), partial pressures, and other factors.

It is noteworthy that most of the bacterially catalyzed reactions discussed above involving the reduction of oxygen, carbon monoxide, carbon dioxide, or sulphate with hydrogen have negative ΔF values, or in other words the reactions yield energy:

I $2H_2 + O_2 = 2H_2O$; $\Delta F_{298} = -$ 113,380 calories

II $3H_2 + CO = CH_4 + H_2O$; $\Delta F_{298} = -$ 35,760 calories

III $4H_2 + CO_2 = CH_4 + 2H_2O$; $\Delta F_{298} = -$ 31,030 calories

IV $4H_2 + 2CO_2 = CH_3COOH + 2H_2O$; $\Delta F_{298} = -$ 20,690 calories

V $4H_2 + H_2SO_4 = H_2S + 4H_2O$; $\Delta F_{298} = -$ 56,750 calories.

In the standard state the formation of formic acid from carbon dioxide and hydrogen requires energy:

VI $H_2 + CO_2 = HCOOH$; $\Delta F_{298} = +$ 6,340 calories.

Ordinarily the reaction would proceed to the left, as indicated by the positive ΔF value, but when the concentration of formic acid is extremely low and the partial pressure of gases is relatively high, ΔF is negative and the reaction has been observed to proceed spontaneously to the right when catalyzed by hydrogenase (68, 79, 156, 186). The synthesis of formaldehyde (or other progenitor of bacterial cell substance) from the reduction of carbon dioxide by hydrogen likewise requires energy (positive ΔF value) under standard conditions:

VII $2H_2 + CO_2 = (HCHO) + H_2O$; $\Delta F_{298} = +$ 6,740 calories.

While the concentration of reactants could be adjusted to make the reaction exothermic, ordinarily bacteria obtain energy from other reactions to synthesize cell substance. This energy can be obtained from the concurrent oxidation of hydrogen by bacteria which catalyze reactions I, III, or V and from other reactions.

Hydrogen production from higher fatty acids requires energy as indicated by reaction IV and the following hypothetical reaction for the fermentation of butyric acid:

VIII $C_3H_7COOH + 6H_2O = 4CO_2 + 10H_2$; $\Delta F_{298} = +$ 53,840 calories.

This reaction will proceed to the right, or hydrogen will be formed, only if considerable energy is available from other concurrent reactions catalyzed by bacteria; or more likely some molecules of butyric acid will be oxidized to lower fatty acids to provide energy for the conversion of a few molecules into hydrogen and carbon dioxide. The ΔF values for the fermentation of glucose (IX), glycerol (X), and other carbon compounds with the formation of hydrogen are positive or only slightly negative as compared with free energy of formation of the reactants:

IX $C_6H_{12}O_6 + 6H_2O = 6CO_2 + 12H_2$; $\Delta F_{298} = -8,580$ calories

X $C_3H_8O_3 + 3H_2O = 3CO_2 + 7H_2$; $\Delta F_{298} = +320$ calories.

Since bacteria are not perfect machines, they cannot be expected to catalyze spontaneously such reactions as IX and X where the $-\Delta F$ is only a small part of the free energy of formation of the reactants. The "free energy efficiency" of bacteria for the few reactions that have been studied ranges approximately from 5 to 30 per cent (6). This helps to account for the relatively low yields of hydrogen obtained from such reactions; most of the organic compound being oxidized to lower alcohols, aldehydes, or fatty acids in order to yield enough energy for the life processes of the bacteria. This is in agreement with experimental data.

The foregoing examples should suffice to illustrate that hydrogen formation from organic compounds by bacteria is a reaction which requires the expenditure of energy. The liberation of hydrogen from methane or other hydrocarbons, which may be energized by alpha radiation (81, 110), also requires energy:

XI $2CH_4 = C_2H_6 + H_2$; $\Delta F_{298} = +16,340$ calories

XII $2C_2H_6 = C_4H_{10} + H_2$; $\Delta F_{298} = +11,520$ calories.

The alpha radiation of any hydrocarbon or other hydrogen-containing compound, including water, results in the liberation of hydrogen, according to Lind (108). He declared that "The absence of hydrogen in natural gases is still anomalous, since we know it must be liberated in the earth's crust. . . ." Some of the reactions summarized above (I–V) which are known to take place under conditions outlined by the "geological fence" (38a) may help to explain the absence of hydrogen as well as the origin of oil.

The positive ΔF values for reactions XI and XII indicate that in the standard state there would be a tendency for higher hydrocarbons to revert to methane, on the assumption that the reactions are reversible. In the standard state reaction XI, for example, would probably go to the left unless the concentration of methane is high compared with the concentrations of hydrogen or ethane. Taking $1.35 \times \log (P_2/P_1)$ as the factor for the free energy of dilution, where P_1 and P_2 are two different partial gas pressures, it is calculated that equilibrium could be established, or ΔF_{298} would equal zero, when the partial pressure of methane is 8.12×10^5 times greater than the partial pressure of either hydrogen or ethane. If the difference in partial pressures is greater than this, the tendency would be for reaction XI to proceed to the right spontaneously in the presence of an appropriate catalyst.

Some theoretical reactions.—Although reactions like XI and XII, in which lower hydrocarbons are converted into higher members of the series, require energy in the standard state, the hydrogen which is liberated provides a potential source of energy when oxidized. For example the formation of one gram-molecule of hydrogen from the condensation of methane, as in reaction XI, requires 16,340 calories of free energy, but the oxidation of this hydrogen by sulphate reducers, as in reaction V, theoretically could produce 16,520 calories. These values can be compared with 11,520 calories required to liberate a gram-molecule of hydrogen from the condensation of ethane, as in reaction XII, and a yield of 7,800 calories of free energy from the oxidation of a gram-molecule of hydrogen to methane, as in reaction III. Assuming such an origin of higher hydrocarbons from the condensation, polymerization, or methylation of lower members of the series, the oxidation of the resultant hydrogen by sulphate reducers or methane producers theoretically could provide enough calories to give favorable free energy balances. Assuming further that additional hydrogen or energy becomes available from other reactions, for example, radioactivity, and that the partial pressures of the lower hydrocarbons are greater than the partial pressures of the higher members of the series, as would be the case if higher hydrocarbons are formed by such a mechanism, the free energy balances may be more than adequate to permit the condensation reactions to proceed spontaneously at ordinary temperatures. These favorable free energy balances, together with the demonstrated ability of bacteria to oxidize hydrogen and the ability of alpha radiations to form higher hydrocarbons from lower members of the series seems to indicate the desirability of thoroughly examining the possibilities of some hydrocarbons having had such an origin.

Lind (107) has asserted that there is a definite chemical reactivity among hydrocarbons, enabling them to spread out in both directions to give a great variety of hydrocarbons found in petroleum. He cites the work of Wilson on the thermodynamics involved to corroborate his hypothesis that the alpha radiation of any single member should result in the formation of all other members of the hydrocarbon series both high and low.

The formation of higher hydrocarbons may be a process of condensation and polymerization of methane and simple hydrocarbons as postulated by Lind (107), or it may involve the reduction and addition of carbon dioxide:

III $CO_2 + 4H_2 = CH_4 + 2H_2O; \quad \Delta F_{298} = -31{,}030$ calories

XIII $CH_4 + CO_2 + 3H_2 = C_2H_6 + 2H_2O; \quad \Delta F_{298} = -14{,}890$ calories

XIV $C_2H_6 + CO_2 + 3H_2 = C_3H_8 + 2H_2O; \quad \Delta F_{298} = -16{,}890$ calories

XV $C_3H_8 + CO_2 + 3H_2 = C_4H_{10} + 2H_2O; \quad \Delta F_{298} = -17{,}010$ calories

XVI $C_4H_{10} + CO_2 + 3H_2 = C_5H_{12} + 2H_2O; \quad \Delta F_{298} = -16{,}500$ calories.

Reaction III is known to be catalyzed by methane-producing bacteria; reactions XIII–XVI or similar reactions may possibly be catalyzed by bacteria, alpha radiations, or other catalytic agents.

The free energy values for the standard state are larger when higher hydrocarbons are converted into lower members of the series, as indicated by reactions XI, XII, and the following hypothetical reactions:

XVII $2C_2H_6+CO_2+4H_2=C_3H_8+2CH_4+2H_2O$; $\Delta F_{298}=-32{,}870$ calories

XVIII $2C_3H_8+CO_2+5H_2=C_4H_{10}+3CH_4+2H_2O$; $\Delta F_{298}=-49{,}390$ calories

XIX $2C_4H_{10}+CO_2+6H_2=C_5H_{12}+4CH_4+2H_2O$; $\Delta F_{298}=-60{,}700$ calories

XX $C_2H_6+CO_2+3H_2=3CH_4+2H_2O$; $\Delta F_{298}=-47{,}570$ calories

XXI $C_3H_8+CO_2+4H_2=4CH_4+2H_2O$; $\Delta F_{298}=-61{,}910$ calories

XXII $C_4H_{10}+CO_2+5H_2=5CH_4+2H_2O$; $\Delta F_{298}=-75{,}430$ calories.

The large negative ΔF values in reactions XVII–XXII suggest that the normal tendency would be for higher hydrocarbons to revert to methane, and this may actually take place unless counteracted by high partial pressures of methane. The partial pressure of methane may be considerably greater in microspheres or structural traps of microscopic dimensions in petroliferous sediments than indicated by the analysis of natural gas.

Though highly hypothetical, reactions XIII–XIX suggest exciting possibilities to account for the formation of higher hydrocarbons from lower members of the series. If such reactions could be catalyzed, hydrogen would be the principal limiting factor in the amount of higher hydrocarbons that could be produced. There are reasons for believing that bacteria may be able to catalyze such reactions, although conclusive proof is lacking. In this connection it is significant to point out that virtually all types of hydrocarbons are attacked by bacteria in the presence of free oxygen (197), a reaction which requires the enzymatic activation of one or more carbon atoms in the hydrocarbon. If such carbon atoms are enzymatically or catalytically activated in the presence of hydrogen at low redox potentials (195), the hydrocarbons may conceivably react with carbon dioxide as indicated by reactions XIII–XXII. Hydrogen may be supplied by the bacterial fermentation of organic matter, various chemical reactions, or by the alpha radiation of compounds containing hydrogen. Such a theory to explain the formation of some petroleum hydrocarbons does not preclude the possibility of others resulting from the degradation or modification of the remains of plants and animals by other processes.

It is the writer's present belief that petroleum has been formed primarily from organic matter by multiple reactions. Part of the hydrocarbons and other constituents of petroleum are synthesized in the cell materials of plants, animals, and bacteria, buried in sediments, and preserved intact. Part results from the degradation and modification of organic matter after its burial in sediments, under the influence of biological, chemical, and physical agents. While much methane may result from the reduction of carbon dioxide by hydrogen, most of the carbon dioxide and a goodly part of the hydrogen probably had an organic origin. The polymerization of hydrocarbons by reactions similar to those outlined above appear to be thermodynamically possible and may occur under certain conditions. Other conditions may be conducive to the fragmentation of larger molecules with the formation of lower members of the series. The transfer of hydrogen characterizes both types of reactions. The evidence seems quite conclusive that bacteria may contribute to the reactions by catalyzing either the formation or the utilization of hydrogen.

SUMMARY AND CONCLUSIONS

A review of the literature reveals that bacteria capable of fermenting organic matter with the formation of hydrogen commonly occur in soil, swamps, sediments, sewage sludge, and elsewhere in nature. More than thirty bacterial species endowed with this ability are listed.

Up to 10,000 hydrogen-producing bacteria per gram have been demonstrated in samples of marine bottom deposits, when treated to inhibit the activity of hydrogen-consuming bacteria which also commonly occur in bottom deposits. Both types of organisms have been found in reservoir fluids and in oil sands.

The formation of free hydrogen is limited primarily by the presence of hydrogen-oxidizing bacteria and the availability of organic matter. Sugars, starches, cellulose, polyhydric alcohols, peptones, amino acids, and fatty acids are fermented with the formation of hydrogen.

Hydrogen production has been observed at redox potentials ranging from $E_h - 0.05$ to -0.45 volt and at reactions ranging from pH 5.5 to 9.8.

Hydrogenlyase and hydrogenase are enzymes which catalyze the liberation of hydrogen, some of the reactions being reversible.

There is generally little or no free hydrogen in marsh gas or other natural gases, in spite of the presence and probable activity of hydrogen-producing bacteria. This is attributed to the microbial utilization of hydrogen as fast as it is produced. Septic samples of soil, sewage sludge, coal-mine water, oil-well brines, and marine muds consume molecular hydrogen.

Several types of hydrogen-oxidizing bacteria are listed, including species which reduce oxygen, nitrate, nitrite, bicarbonate or carbon dioxide, carbon monoxide, sulphate, sulphite, thiosulphate, various amino acids, aldehydes, alcohols, carboxylic acids, and other compounds. Of particular interest are various hydrogen-oxidizing anaerobes which convert bicarbonate or carbon dioxide into methane, simple carboxylic acids, or other compounds. Such bacteria may help to account for the general absence of hydrogen in natural gas, the porosity of limestone, and the origin of oil. Certain sulphate reducers found in sediments also oxidize hydrogen with the formation of hydrogen sulphide. The general occurrence of free hydrogen in igneous rocks as contrasted with its relative absence in sediments supports the view that bacteria eliminate hydrogen.

Hydrogen may be generated by chemical reactions in the earth's interior, by the alpha radiation of compounds containing hydrogen, and by bacterial activity. Besides contributing to the generation of hydrogen, radioactivity may energize the polymerization or condensation of simple hydrocarbons into higher members of the series. The free energy values of several reactions involving hydrogen transfers, some of which are known to be catalyzed by bacteria, are calculated to demonstrate the possible importance of such reactions in the origin of oil.

Whether the hypothetical reactions involving the transfer of hydrogen result in the formation of higher hydrocarbons or lower members of the series would depend partly on the concentration (activity) of the reactants and partly on the availability of energy. It is estimated that the bacterial oxidation of hydrogen could provide the necessary energy, not to mention the energizing influence of radioactivity and other catalytic agents.

While such reactions could conceivably account for the formation of some petroleum hydrocarbons, it is believed that the great bulk of the hydrocarbons and other constituents of petroleum result from the degradation, transformation, or hydrogenation of organic matter by other mechanisms.

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THE ROLE OF SNAPPING SHRIMP (CRANGON AND SYNALPHEUS) IN THE PRODUCTION OF UNDERWATER NOISE IN THE SEA

MARTIN W. JOHNSON, F. ALTON EVEREST, AND ROBERT W. YOUNG

Scripps Institution of Oceanography of the University of California, La Jolla, California,
Moody Institute of Science, Los Angeles 25, California, and U. S. Navy
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MARTIN W. JOHNSON, F. ALTON EVEREST, AND ROBERT W. YOUNG*

Scripps Institution of Oceanography of the University of California, La Jolla, California,
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Electronics Laboratory, San Diego 52, California

INTRODUCTION

The sea has long been looked upon as a realm of silence. That this view is no longer tenable has been abundantly demonstrated as a result of extensive investigations with modern underwater sound detecting gear. These investigations, which during World War II became of grave importance because of submarine warfare and harbor defense, have shown that great stretches of numerous coastal areas are exceedingly noisy, periodically or perpetually, due to marine animals. Conversely, the investigations also indicate that vast areas of the deep ocean and of shallow water in higher latitudes are indeed notably silent.

The most widespread by far of all the biological underwater noises now known to exist in the sea is a crisp, high frequency, crackling noise caused by snapping shrimp. Examples of these animals are shown in Figures 1 and 2. It was not, however, until the second world war that the extent and persistence of this strange noise was realized and its cause determined. It has now become widely known as "shrimp noise" or "crackle."

The present report is intended to discuss, mainly, the cause and extent of crackle and to present the biological implications that explain its persistence and geographical distribution. Full details of the spectrum of the sound will be dealt with in another report (Everest, Young, and Johnson, in press).

EARLY HISTORY OF SHRIMP NOISE

Before discussing the recent investigations that led to identification of crackle, it will be instructive to review briefly some of the early references that no doubt pertain to this noise phenomenon.

1. Mariners operating small vessels in tropical waters have sometimes reported hearing strange crackling noises within the holds of their craft. The most common

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[1] The work forming the basis of this report was done under contracts OEMsr–30 and NObs–2074 respectively with the Office of Scientific Research and Development (Section 6.1 NDRC) and the Bureau of Ships, Navy Department, while the authors were members of the staff of the University of California Division of War Research at the U. S. Navy Radio and Sound Laboratory, San Diego, California. The following organizations cooperated in the collection of much of the data upon which this report is based: Navy Department, especially the Bureau of Ships; Naval Ordnance Laboratory; the U. S. Navy Radio and Sound Laboratory (now the U. S. Navy Electronics Laboratory); the Scripps Institution of Oceanography; the Coast Guard; and the Columbia University Division of War Research.

explanation given was that the noise was caused by shipworms (teredos) working in the ship's timbers, or that it was due to superficial fouling growths on the hull. It is now known that the crackle from nearby shrimp beds is audible through the hull and probably forms the basis for these stories.

2. The U. S. Coast and Geodetic Survey encountered troublesome noises while engaged in radio acoustic ranging off Oceanside, California in 1933–34. The sound was described as being similar to static crashes or to coal rolling down a metal chute. No explanation could be found for the noise, though efforts were made to correlate it with meteorological and hydrographic conditions, and with road traffic on a highway adjacent to the coast (Comdr. O. W. Swainson, 1943, personal correspondence). Subsequent surveys have demonstrated that shrimp crackle is conspicuous in the area where these observations were made, and is loud enough in some spots to be audible to the unaided ear above the surface during calm water. Dredgings, also, showed the animals to be present in the shale bottom, which is honey-combed by molluscan bores.

3. A U. S. submarine operating in Macassar Strait off Balikpapan early in 1942 circled an area from which a strange crackling noise was emanating. Lt. Comdr. W. D. Wilkins, in reporting this experience, suggested that "the Japs may have some newfangled gadget that they drop." Snapping shrimp are common in the Balikpapan region and the type of bottom and depth of water off Balikpapan form a favorable habitat for them. Other reports from submarine officers strongly suggest that noises often encountered in coastal waters in lower latitudes are attributable to shrimp.

4. Sounds were heard through the hull of a small vessel in Beaufort Harbor, N. C. and in calm water off Cape Hatteras (Hulbert, 1943). These sounds were described as similar to that produced by "dragging a blackberry vine." No doubt they were produced also by snapping shrimp for these animals are abundant in Beaufort Harbor and are now known to be very noisy there. They also occur in offshore waters at Cape Hatteras (Hay and Shore, 1916).

To summarize the above as well as other data, it is apparent from what is now known that the crackling noise has been attributed erroneously to various other phenomena. Some of these are (a) static crashes, (b) rolling pebbles, (c) surf, (d) volcanic or terrestrial disturbances, (e) shipworms working in a wooden hull, (f) superficial fouling on the hulls of ships, (g) noises due to expansion or contraction of the ship's structure, and (h) clapping of oyster or clam shells.

The sharp "snap" produced individually by these shrimp when captured has long been known, and has often been heard during low tide in some areas. The sound has hitherto, however, been considered only a biological curiosity and not a source of significant underwater background noise. Biological sounds similar to shrimp noise will be discussed later.

Recent Investigations

Early in 1942 investigations of underwater ambient noise were begun by the University of California Division of War Research in the San Diego region. From the beginning of field tests a characteristic crackling noise of great magnitude was observed. It was first encountered at various locations off Point Loma and in the San Diego Yacht Harbor, and was found later in coastal waters off La Jolla. Oceanside, and other places on the southern California coast. The origin of the noise was a profound mystery until the end of 1942 when the cause was finally determined.

Identification of the noise was accomplished through laboratory tests of various animals and through field studies in many different habitats and over different populations. In the laboratory the animals were usually tested in large concrete tanks supplied with running sea water. Large public aquaria were also used.

For the listening tests and the exploratory studies, a simple crystal hydrophone and battery operated amplifier system sufficed. The equipment used for sound spectrum measurement in the field consisted of a non-directional hydrophone, a sound analyzer which was capable of selecting the various frequency bands (usually 50-cycles wide or a half-octave), and a graphic level recorder.

The sound emitted by an individual shrimp is a single sharp "snap" or "crack" produced only occasionally. It is the combined snapping of the members of a large population that results in a continuous loud underwater crackle over or near shrimp beds. In the audible band the crackling sound is comparable to the explosive noises produced by brisk burning of large quantities of dry twigs or frying of fat. Similar sounds can be heard by heterodyning ultrasonic bands in the 20–50 kc region down to the audible range. With increasing distance from the source, the sounds merge into a sizzle and finally a hiss without distinct cracks.

Sound spectrum analysis of crackle in the sea reveals that the shrimp noise has its strongest components in the higher frequencies. In contrast to shrimp noise, the noise produced by fish (Loye and Proudfoot, 1946, and Dobrin, 1947) is made up of low frequency sounds and is markedly seasonal and diurnal. In normal "water noise" resulting from waves and streaming of water, the maximum energy is also in the low frequencies. Because of this, shrimp noise is easily distinguished from both fish noise and water noise.

Figure 3 gives an idealized average of the sound spectra observed over shrimp beds in a variety of places. The ordinate for the sound measurements is sound pressure spectrum level.[2]

For comparison, the dashed curve shows the typical water noise observed in the deep sea, where there are no biological noises, for a state 1 sea.[3] This water

[2] Sound level is given as a number of decibels (db) above some reference value which in the present work is a root-mean-square sound pressure of 0.0002 dyne/cm^2. This reference pressure is commonly incorporated in the calibration of sound-measuring instruments, but is frequently not explicitly stated. As a consequence, the decibel appears to be used with two meanings: a unit for an absolute measurement (with a reference value stated or only understood) and a unit for the *relation* of two sounds. In this paper when a sound *level* is stated in decibels it is in the first sense; the second sense is meant when a *change* or *difference* is given in decibels.

The decibel (db) is a logarithmic measure of power ratio (or ratio of pressure squared) such that a 100-fold increase in power (or 10-fold increase in pressure) corresponds to 20 db A doubling of power is an increase of 3 db. A doubling of sound pressure is an increase of 6 db. The smallest change in noise readily perceptible to the ear is of the order of 1 or 2 db

The noise being dealt with here is conceived to be comprised of a rather continuous distribution of sound vibration frequencies. The words "pressure spectrum level" refer to the effective sound pressure level for that sound energy contained in a band 1 cycle per second wide centered at the frequency indicated.

[3] The "sea" as used here refers to waves which are still growing because of the wind, and as such represent an additional motion superimposed upon the swell. A state 1 sea corresponds to waves from crest to trough less than 30 cm. high. See *Instructions to Marine Meteorologica Observers.* U. S. Weather Bureau No. 1221, June 1941, p. 54.

ioise increases at all frequencies with increasing roughness of the sea. It is ap-arent that at the lower frequencies the ambient noise over a shrimp bed is largely letermined by the water noise found everywhere in the sea. However, above 2,000 ycles per second shrimp noise completely overrides the usual water noise. Above 0,000 cycles per second (10 kc) shrimp noise is some 30 db above the noise of a tate 1 sea. The shrimp noise in the region of 10 to 20 kc exceeds the noise in quiet sea by roughly the same amount as the audible noise in a factory exceeds he usual noise in a quiet residence without radio in operation. Because shrimp ioise is greater than the water noise by such appreciable amounts, it is convenient o use an average spectrum level in the vicinity of 10 kc in studying noise suspected f being caused by shrimp. An average of the levels at 3, 5, and 10 kc has been ised for this purpose, and also an average at 10, 15, and 20 kc; the latter has been rbitrarily selected for the present paper.

Analyses were made, also, of single shrimp snaps by taking oscillograms of he sound from isolated identified specimens. The shrimp were placed in a gauze iet within a rubber bucket filled with sea water. The whole assembly was lowered nto a fresh water lake, then the net was drawn from the bucket by means of a ord. Contact with fresh water stimulated the shrimp to snap and photographs vere made of the snap impulses shown on the oscillograph screen.[4] The whole nap lasts about ½ to 1 millisecond. Further details are to be found in the acousti-al report (Everest, Young, Johnson, in press). It is sufficient to note here nainly that the spectrum of a single snap, derived by a Fourier integral analysis, grees qualitatively with the average spectrum over a shrimp bed.

It is not possible to reproduce in the laboratory the extent of crackle heard over hrimp beds in nature, or to simulate the hiss heard at a distance from the bed. herefore, corroborative evidence must come from correlated field observation and pectrum measurements as discussed later.

The explanation of the local underwater sound mystery shed light on a number f qualitative reports of the type discussed in the previous section. Ultimately, it nade possible the prediction of this type of ambient noise in other areas.

Sound surveys made since 1942 in widely separated areas along the East and Vest coasts of the United States from Key West to Chesapeake Bay and San iego to Puget Sound, in the Bahamas, and in the Central and Southwest Pacific ave confirmed the predicted, widespread distribution of shrimp crackle in localities hat are ecologically suitable for snapping shrimp, and its absence in other situations. n the following section an explanation of the relationships is given.

The Biology of Snapping Shrimp and Its Relation to Sound Levels

The geographic locations of noisy crackling areas in the sea and the stability f the sound in these areas are so closely bound to the snapping habit and to the ving requirements of these animals that it is necessary to consider their biology some detail in order to elucidate these problems.

iological relationships

Technically, the snapping shrimp are related to the commercial shrimp, which ey resemble in general appearance. In life habits and details of structure, how-

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[4] The assistance of T. F. Johnston and T. McMillian in this phase of the work is grate-lly acknowledged.

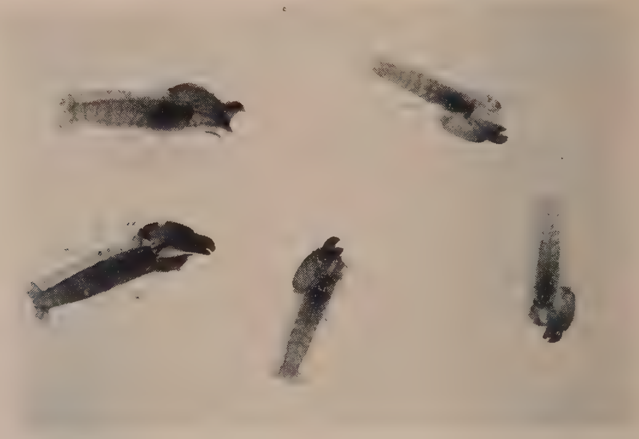

Figure 1. *Synalpheus lockingtoni* natural size. Photographed from live specimens. At upp
left: specimen with claw open to snap.

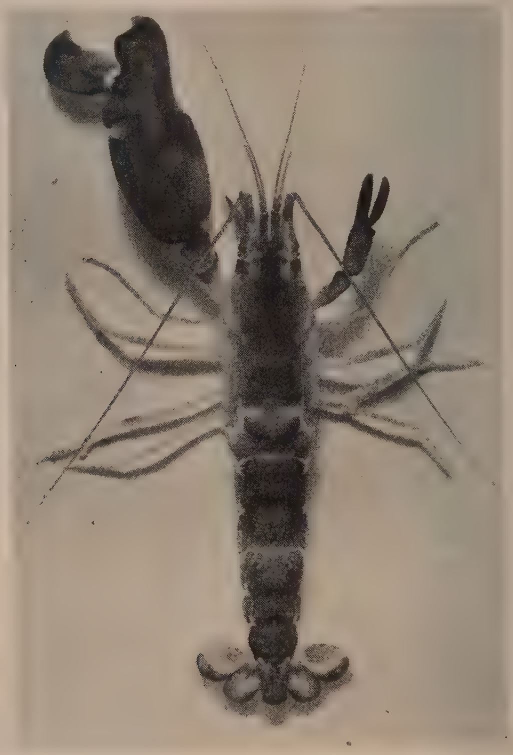

Figure 2. *Crangon californiensis* 2 ×.

ever, they are very unlike the common shrimp. The snapping shrimp family Crangonidae (Alpheidae, see Rathbun, 1904) comprises about 27 genera and numerous species. Of these only the species of two genera, viz., *Crangon* (also called *Alpheus* by many authors) and *Synalpheus*, are capable of vigorous snapping. In the literature there are recorded about 215 species of *Crangon* and 150 species of *Synalpheus*. Two species of these genera are shown in Figures 1 and 2.

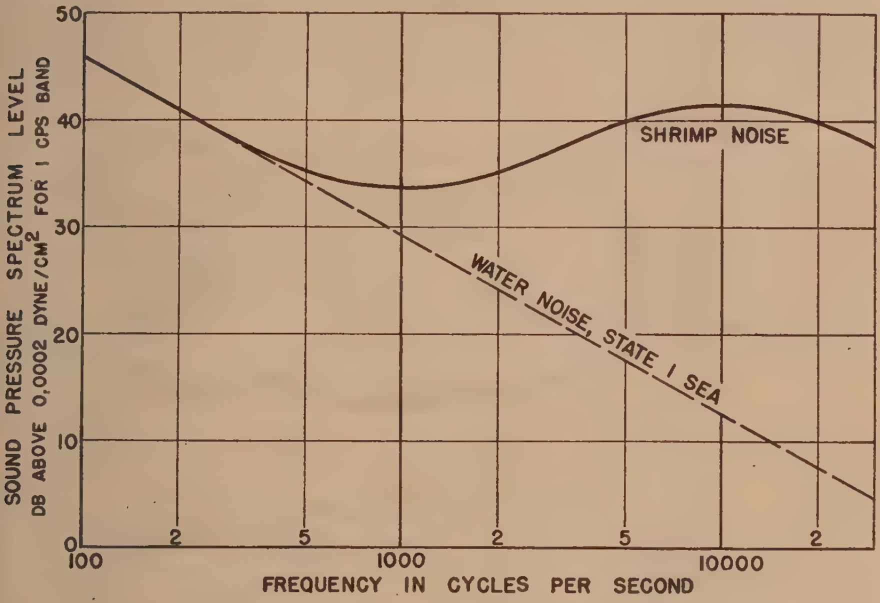

FIGURE 3. Average ambient noise spectrum over shrimp bed.

The snapping habit

Studies of most species of these two genera have been based on preserved specimens; consequently, the snapping has not been observed directly in many species. The claw structure, however, indicates that all the species do snap to some extent. The species range in size from about 2 cm. to a giant species, *C. strenuus,* attaining a length of 8 cm., but it is clear that size is not necessarily correlated with the noise produced. The few direct sound measurements available of isolated specimens indicate, for example, that *Synalpheus lockingtoni* may produce a louder snap than its larger relative *Crangon dentipes*. The average peak pressure level of *Crangon* for a distance of a meter was 115 db above 0.0002 dyne/cm.^{2}; whereas it was about 124 db for *Synalpheus*. While the difference may be real, the present observations are too few, and the spread too great, to confirm this.

The habit of snapping is associated with defensive and offensive activities. In closing the snapping claw, a vigorous jet of water is produced by means of a plunger arrangement described below. This sudden gush of water serves to frighten away enemies approaching too near. The antagonist may also be driven away or sometimes killed by a direct blow of the small hammer, but the biological significance of the accompanying loud sound is uncertain.

The snapping mechanism

A good deal has been written regarding the sound-producing mechanism, especially by Coutière (1899), Brooks and Herrick (1894), and Volz (1938). This mechanism consists of one disproportionately large hard appendage comparable to one of the large "claws" of the lobster. Figure 4 shows an enlarged drawing of the snapping claw of *Crangon californiensis*, a vigorous snapper (*cf.* Fig. 2).

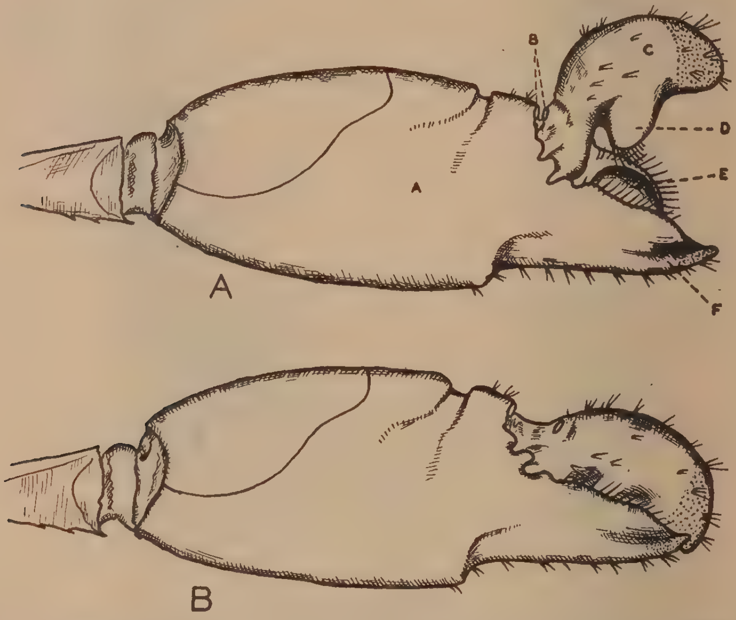

FIGURE 4. *Crangon californiensis*. Snapping mechanism. *A*, Snapper open; *B*, Snapper closed —A, palm; B, suckers; C, movable finger; D, plunger; E, socket; F, thumb.

In some species, the snapping claw is nearly as large as the body of the animal, giving ample room for development of strong snapping muscles. A movable hard "finger" (C) is jointed near the outer end of the "palm" (A) of the claw forming a forceps-like arrangement with the immovable "thumb" (F). On the inner side of the finger is a plunger-like structure (D) which fits into a socket (E) in the thumb. Leading forward from the socket is a groove through which the water escapes when the plunger is suddenly forced into the hollow. When the finger is raised, the plunger is withdrawn from the socket, and it has been held by some early observers that the noise is produced by this action, similar to the "pop" heard when a cork is suddenly pulled out of a bottle (Wood-Mason, 1878). The biological function of the plunger-socket arrangement, however, is the production not of sound, but of the water jet mentioned above. It may aid, also, in preventing dislocation of the finger when it is violently snapped.

The plunger-socket device is present in both *Crangon* and *Synalpheus*. In all species of *Crangon*, there is also a "sucking" disc on the outer side of the finger near its point of attachment (Fig. 4A). When the finger is fully raised, this disc contacts precisely a similar disc on the palm so that the two are firmly in contact when the finger is in position to snap. These suckers serve as a trigger to hold the finger back, and extra muscular tension must be exerted in breaking the contact. This in turn increases the force of the impact. The suckers are absent in *Synalpheus*, but in the same relative position there are smooth surfaces that contact perfectly. These surfaces probably serve the same purpose as the suckers. That the suckers on the claw of *Crangon* do serve as a restraining trigger is readily demonstrated. When the finger of a dead specimen is forced back to its fullest extent, it is held there so firmly that some force is needed to break the contact. This was demonstrated even in a specimen that had been preserved in formaldehyde for several months.

The precise way in which the sound is produced is still a matter of some doubt. The best explanation appears to be that the sound is produced by impact as the movable finger strikes a glancing blow on the opposing tip of the thumb. The tips of these structures are either very heavily calcified as in many species of *Crangon*, or are tipped with a heavy formation of chitin as in *Synalpheus lockingtoni*.

In a painstaking investigation of *Crangon dentipes* and *Synalpheus laevimanus* of the Mediterranean, Volz (1938) found a small chitinous ridge at the inner upper margin and back wall of the socket. This ridge, he concluded, is part of a breaking device which incidentally aids in producing the sound when it is struck by the plunger as it forcibly enters the socket.

It is of passing interest to note that the snapping claw may be either right or left; if it is lost through injury the inconvenience is only temporary, because a new one is promptly grown in the first or second moulting when the shrimp sheds its old shell. In this process of renewal, however, the original large claw is replaced by a small one, while the former small pinching claw is enlarged and becomes the new snapping claw (Wilson, 1903).

Type of habitat and crackling areas

The species of *Crangon* and *Synalpheus* are bottom-living animals living mainly below zero tide level and, though capable of swimming, they rarely do so in the adult stage. They are notably secretive and demand ready-made or easily maintained burrows. Hence, they seek concealment in crevices and holes provided by coral, stones, shells, calcareous algae, and other solid objects. It has been demonstrated repeatedly by collectors that they live preponderantly on these bottom types. This habit renders collecting very difficult in most instances, especially when a dredge must be used. Hence the animals are far more abundant than generally realized.

In the East Indies they are especially fond of bottoms covered by the calcareous alga *Lithothamnion* (de Man, 1916). They commonly live among the roots of eel grass and holdfasts of seaweeds and among mussels, barnacles, and other substantial fouling organisms on wharf piles, etc. Some live in the channels and pores of living sponges. In many of these situations there can be heard a continuous fusillade of snapping. Where sound measurements have been made at old heavily-fouled piers, the spectrum level in the region of 3 to 10 kc has reached about 60 db above 0.0002 dyne/cm^2.

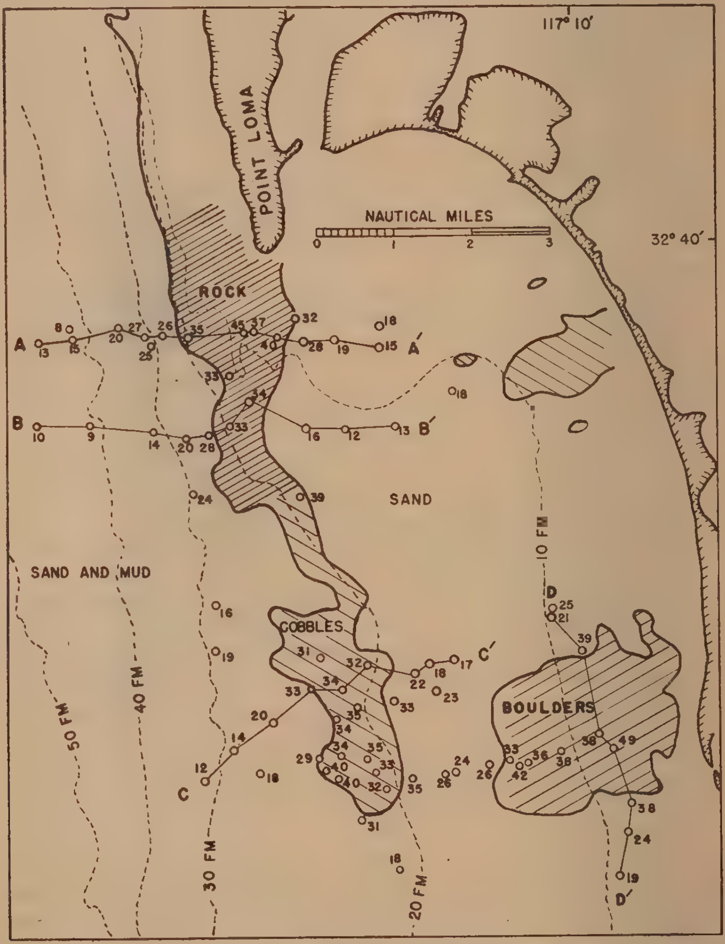
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FIGURE 5. Locations of series of stations occupied for sound level measurements across areas ecologically favorable to snapping shrimp. The number adjacent to each station is the average of the 10, 15, and 20 kc spectrum levels.

Snapping shrimp do not normally live in any significant numbers on extensive sand or mud bottoms without some sheltering materials. However, some species (for example, *Crangon californiensis*), tolerate muddy conditions among eel grass, etc., and have been dredged with mud, particularly in harbors littered with solid debris. Crackling is intensive in some of these situations. A European species, *Crangon ruber,* is said to be "not uncommon" on the mud bottom off Ram's Head near Plymouth, England and in the Mediterranean. No information is available regarding the underwater sound produced by this species.

The way in which the crackling noise increases over a habitat favorable to shrimp is indicated by Figures 5 and 6. Figure 5 shows some of the stations in the San Diego area at which sound spectrum measurements were made under careful control. The number adjacent to each station is the average of the 10, 15, and 20 kc spectrum levels. Water depths may be estimated from the depth contours. The bottom character here is well established.[5] There is a clearly defined stretch of shale which is well honey-combed by abandoned mollusk borings in which the shrimp find retreats. Continuous with the shale is a less regular stretch of cobbles. Nearby is an isolated patch of boulders. Dredgings reveal all these to be populated by shrimp in contrast to dredgings from the surrounding sand-mud and sandy areas of comparable depths.

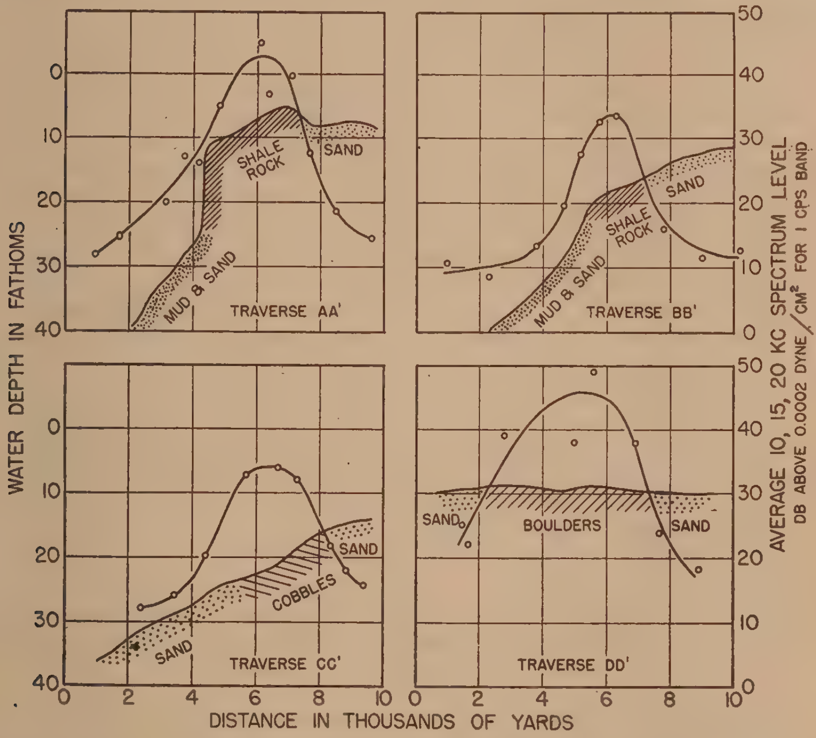

FIGURE 6. Profiles of bottom at stations occupied in Figure 5 showing spectrum levels across shrimp beds.

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[5] The assistance of Dr. F. P. Shepard in these studies is gratefully acknowledged.

The sound levels between the cobbles and boulders are higher than would be expected over sand, but this apparently results from a combination of sound transmitted from both areas since the positions are well within the sound range of both.

Specific traverses are indicated by *AA′*, *BB′*, *CC′*, *DD′* in Figure 5. The corresponding depth profiles (use left-hand scale) are given in Figure 6 along with the average 10, 15, 20 kc spectrum level (right-hand scale) at each station.

These show how markedly the sound, in the frequency range 10–20 kc, rises in passing over the shrimp habitats. During low sea states, the transmitted shrimp sound is appreciable to a distance of over a mile from the boundary of the bed.

Similar sound spectrum measurements were made at numerous shallow and deep water stations at widely scattered localities on the east Pacific coast, among the Pacific Islands[6] and along the west Atlantic coast and the Bahamas.[7] A typical set of observations, from six stations off Barbers Point, Oahu Island, is given in Figure 7. The coral, algae, and shell bottom extends into deep water, yet the sound level falls off rapidly in depths greater than 30 fathoms, despite a bottom type favorable to shrimp. At the outermost station the shrimp noise presumably merged with the normal ambient water noise.

An average 10, 15, 20 kc spectrum level of 30 db was arbitrarily chosen as a dividing point for sorting the observations, values greater than this being designated "high" and those less as "low." When the data from both the Pacific and Atlantic were studied with regard to bottom type, it was found that within 0–30 fathoms about 80 per cent of the "high" levels were observed over bottom types favorable to shrimp. In contrast, about 90 per cent of the "low" sound levels (below 30 db) for this depth zone were over unfavorable bottom. In view of the difficulty of establishing precisely the character of the bottom over considerable areas, this correlation is surprisingly good.

Depth distribution

Data on hauls of snapping shrimp, taken at various depths, are scattered widely throughout the biological literature (de Man, 1916). Table I shows how 185 species of *Crangon* and *Synalpheus* have been reported as occurring in five depth zones. The table includes only trawling and dredging collections from the bottom.

TABLE I

Distribution of 185 species of Crangon *and* Synalpheus *reported from 5 depth zones*

Bottom depth zone	Number of times shrimp reported	Number of species
0–30 fathoms	418	171
30–70	101	59
70–100	5	4
100–250	14	9
Over 250	7	4

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[6] Many of these field data were collected by W. E. Loomis of the Naval Ordnance Laboratory during a survey in cooperation with that organization.

[7] These observations were made in cooperation with the Columbia University Division of War Research, Bureau of Ordnance and the Naval Ordnance Laboratory.

While most of the species are reported in 0–30 fathom water, it cannot be concluded that Table I gives the actual distribution, since it is not possible to know precisely how uniform the effort and efficiency of collecting have been in various zones. Presumably, it has been roughly comparable with respect to the number of hauls in the first two zones. This is supported by a summary of 3,483 hauls by various expeditions that have contributed to the study of these animals. Among these expeditions are especially those of the USS "Albatross" (1883–1911), the "Siboga" (1899–1900), the "Percy Sladen" (1905), and the "John Murray" (1933–1934). An analysis shows that 17 per cent and 20 per cent of the hauls were taken respectively in the 0–30 fm. and 30–70 fm. zones. The remainder were in deeper water. Thus the table gives a fair idea of the depth distribution and indicates that the largest populations are in the 0–30 fathom zone.

Acoustic data support this belief, for in water deeper than 30 fathoms the sound levels are low (except where sound is transmitted from nearby shrimp beds), even though the bottom type is favorable for shrimp, as in Figure 7. It is probable that the deeper ranging species have their maximum concentration in depths less than 30 fathoms, and that the typically deep water forms do not occur in sufficient concentrations to produce a continuous crackle like that heard in shallow water.

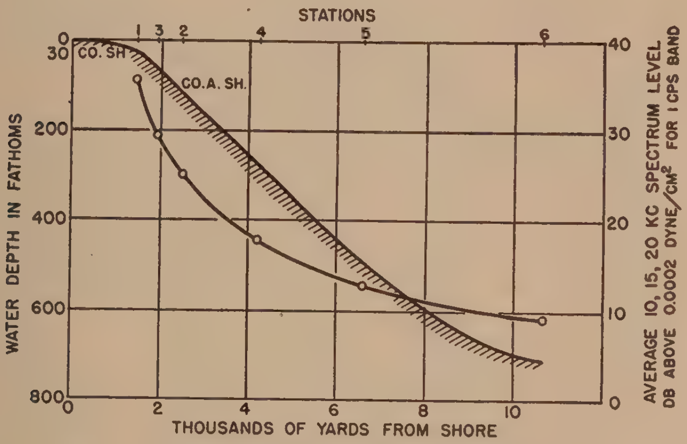

FIGURE 7. Sound observations from Barbers Pt., Oahu showing drop in spectrum level with depth of water and distance from shallow (less than 30 fm.) areas favorable to snapping shrimp.

Life history and its bearing on continuity of crackle

The bedlam of crackling noise over a shrimp bed is never ending. This continuity is correlated with the life history and stability of shrimp populations. The fertilized eggs of snapping shrimp are carried by the adult female until they hatch as free-swimming larvae about 4 mm. in length. After a period of drifting with the water currents, the larvae settle to the bottom and assume the structural characteristics and habits of the adults. No snapping is possible until this time. The free-floating period serves to disperse the animals widely and they thrive after settling to the bottom where living conditions are favorable for adults. From what is known of a few species, there appears to be a long breeding season in low latitude waters. Gravid specimens have been found in all seasons at La Jolla. Near the higher latitudes the breeding season is probably shorter.

The duration of life of the individual is not known, but adults collected at La Jolla, California, in December 1942, and January 1943, were still thriving in an aquarium after twenty-two months of captivity. These facts are mentioned because the maintenance of overlapping generations is, no doubt, important in explaining the seasonal continuity of the crackling sound. A short breeding season and a short span of life would result in a considerable variation of the adult population and this, in turn, would be expected to cause an appreciable seasonal variation in shrimp noises. No seasonal variation of this nature has yet been noticed.

Observations have not revealed any swarming or migratory movements such as characterize many other marine animals during the breeding season, and this, too, is correlated with the small fluctuations in sound level.

The snapping shrimp are gregarious to the extent that large numbers of a given species are found either in pairs or as solitary specimens in isolated retreats within the area. The occupants of these retreats make a noisy protest when an intruder approaches. Specimens have been observed to leave their burrows for short journeys in search of food, especially at night, but those under observation always returned to their respective retreats. These retreats in some instances were occupied steadily by the same specimen for several months. *Crangon californiensis* showed a much stronger tendency to desert its burrow than did other local species observed.

There is a small diurnal variation in shrimp noise. At night the levels are 2 to 5 db higher than in the daytime. In addition, there is a slight peak in the noise level shortly before sunrise and after sunset. The effect is caused, probably, by increased activity of the shrimp at these times. In the laboratory tanks the shrimp appear to increase their search for food at night. This is also a well-known behavior among many other marine animals. Thus, the overall increased activity would lead to more irritation and more snapping.

It should be noted that an increase in sound level of 3 db actually represents a two-fold increase in shrimp activity.

Observations made so far have indicated no appreciable seasonal variation in shrimp noises. This is in agreement with the known stability of the adult population discussed above. This result may not apply near the edge of the shrimp belt, however, or at unusual localities inside the belt having large seasonal variations in water temperature.

Geographical range of shrimp correlated with distribution of crackle

The species of *Crangon* and *Synalpheus* are confined to coastal or shallow water throughout the tropical and subtropical regions. This type of distribution is, no doubt, governed by water temperature, but precisely how this operates is not yet clear. In general, the 11° C. winter surface isotherm marks the approximate northern and southern limits of their continuous range (Fig. 8). In Figure

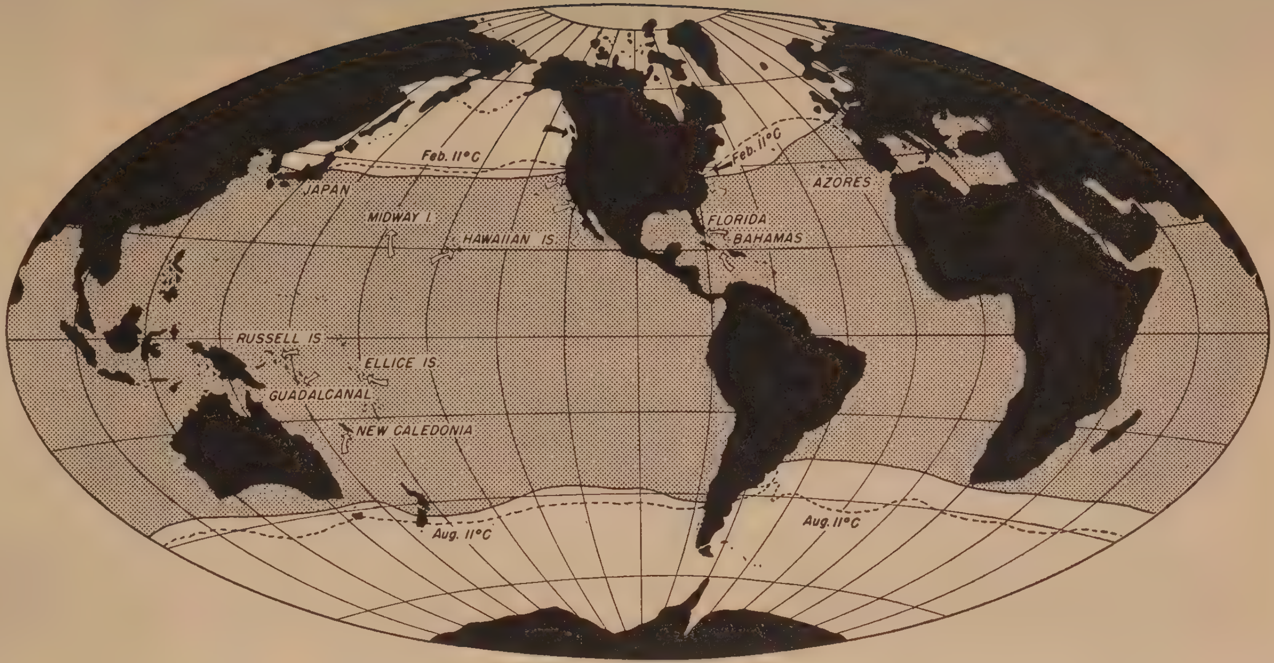
Feb. 11°C
Feb. 11°C
JAPAN
AZORES
MIDWAY I.
FLORIDA
HAWAIIAN IS.
BAHAMAS
RUSSELL IS.
ELLICE IS.
GUADALCANAL
NEW CALEDONIA
Aug. 11°C
Aug. 11°C

FIGURE 8. Geographical range of snapping shrimp (*Crangon* and *Synalpheus*). These genera are found within the shaded area where depth and bottom conditions are favorable. The arrows denote general areas where ambient noise has been measured.

8 this range is represented by the shaded area. The thermal control of distribution must, however, be a complex one. It is not accomplished simply by the temperatures falling to or below this level during the winter. Certain critical periods of life such as spawning and larval development appear to require a considerable period of warmer temperatures, near or above 17° C. during the summer. The isolated populations lying outside of the 11° C. isotherms are probably governed by favorable local conditions. Examples of this sort are seen at the north end of Honshu, near Vladivostok, and along the coast of Ireland. A comprehensive study of the literature giving the localities where snapping shrimp have been collected one or more times, shows them to be present in all tropical and subtropical locations where extensive surveys for crustacea have been made. In the strictly tropical and subtropical waters, the distribution of shrimp is believed, therefore, to be continuous within the areas where depth and type of bottom are favorable. This agrees with the available acoustic data from sound surveys made in various parts of the world.

There is but little quantitative information on geographical distribution. The animals are, as a rule, difficult to collect in representative numbers because of their habits of seeking retreats in hollows and crannies of rock, coral, etc. It seems clear, however, that the greatest number of individuals as well as species occur in tropical waters among coral and other reef organisms. The northern and southern boundaries of continuous distribution along the open coast are, no doubt, transition zones in which the populations become progressively sparser, but how wide these zones are is not known. However, the animals are known to be quite abundant at Beaufort, N. C. and at Monterey Bay, California, and listening tests in these areas reveal shrimp crackle to be pronounced, though spectrum measurements are not available. The region between Cape Lookout and Wimble Shoals on the east coast and the region of San Francisco on the west coast represent the border of distribution (Hay and Shore, 1916; Schmitt, 1921). Sparse crackle has been heard in these regions, but sound measurements fail to show the characteristic spectra of shrimp noises. Acoustically, there must be a certain minimum concentration of shrimp in a given area before the snapping sound can materially influence the reading of instruments which require an appreciable time to respond. Sound measurements from latitude 9° S. to 33° N. indicate about the same levels over shrimp beds irrespective of latitude.

Biological Sounds Similar to Shrimp Noise

Among the known animals producing noises that may be confused with shrimp crackle or that may in a minor way contribute to the ambient noise are the following:

Gonodactylus oerstedii (and no doubt other species of this genus), a crustacean generally known as "mantis shrimp" or "squillid," makes a clicking sound when striking out with its claws. Like the snapping shrimp, this animal has a wide tropical distribution and lives in similar habitats.

At least two species of the *Coralliocars* shrimp, *C. graminea* and *C. wilsoni,* are capable of snapping by means of a structure similar to that used by regular snapping shrimp. They are not known to be abundant and apparently have a geographic and habitat range falling within that of the snapping shrimp.

Typton spongicola of the Mediterranean and *Pontonia pinnae* of East Africa are species of crustacea said to be capable of snapping. They are not considered numerous.

The larger crabs such as *Cancer* and *Portunus* have been observed to make noises sounding like the individual crack produced by *Crangon* and *Synalpheus,* but the noise is incidental to the cracking of brittle shells of small clams, etc., for the food within the shell. Crackling from this source can, of course, be present only as long as shell food is being eaten. Other animals, including fishes, which occasionally crack shells for food would also fall into this category of incidental noise makers. To produce the volume of crackling that occurs continuously over shrimp beds would, however, very quickly exhaust all available shells. Hence cracking of shells is believed to be a very small contribution to the ambient noise.

The trigger fish is said to be capable of making a clicking sound by means of the joints of some of the fin spines; the mackerel by means of its pharyngeal teeth.

Populations of barnacles produce very weak crackling sounds, barely audible at very close range. Barnacles and perhaps other larger crustacea (preening their shells or feeding) appear to be the main cause of these very faint noises sometimes heard when the hydrophone is within a few feet of the shore in quiet waters north of the geographic range of snapping shrimp.

In the Hawaiian area, a very troublesome raucous noise with a sharp high peak at 3 kc has been encountered. This has been called "evening noise" in view of its regular occurrence each evening between about 7:30 and 10:00 P.M. In one harbor, this caused a 10 db rise in overall level of the ambient noise during the evening hours. The origin of the noise was not determined, but the possibility of its being somehow associated with increased shrimp activity at a distant bed in the evening has been suggested. However, an obvious difference in character between shrimp noise and "evening noise" militates against this explanation.

Conclusions

1. The sea is far more noisy, as a result of biological noises, than was commonly believed.
2. The most widespread of the biological underwater sounds is a continuous high frequency crackle caused by snapping shrimp (*Crangon* and *Synalpheus*). The continuity of high magnitude sound produced by populations of these animals appears to have no counterpart in biological nature.
3. All shallow water areas (0–30 fathoms) within the geographical range of *Crangon* and *Synalpheus* and with bottom conditions and temperatures favorable to these animals are likely to be noisy.
4. The strongest components of shrimp noise are in the frequency range 2 to 15 kc.
5. The sound levels over snapping shrimp beds are usually 30 db higher than state 1 sea noise.

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Contribution No. 336

AGAR

by C. K. Tseng

AGAR, or Agar-Agar, is a gelatinelike product of red seaweeds, made from *Gelidium* and other agarophytes (agar-bearing plants) such as *Gracilaria, Ahnfeltia* and *Pterocladia*. It is best known as a bacteriological culture medium, and is extensively used for food, as roughage, and in making jelly desserts, confectionery, icings, salad dressings, and dairy products. It is employed in canning meat and poultry, in laxative preparations, as a constituent of medicinal pills and capsules, in numerous pharmaceutical and cosmetic creams and jellies, as a dental impression mould base, and in wire-drawing lubricants. Agar is prepared by boiling the agarophytes in water and subsequently purifying and drying the product. It is produced chiefly in Japan, and also in China, Russia, the United States, Mexico, South Africa, New Zealand and Australia. It is amorphous and translucent, and may be found on the market in the form of powder, flakes, shreds, or bricks. Agar is insoluble in cold water, but swells considerably, absorbing as much as 20 times its own weight of water. It readily dissolves in boiling water, and is able to set to a firm gel at concentrations as low as ½%. Although a 1% agar sol solidifies at about 104° F., its gel does not melt until about 203° F., showing a striking case of hysteresis. Agar gels carry small negative electric charges. Like other gels, they exhibit syneresis. Chemically, agar is the sulphuric ester of a linear galactan, consisting of a long chain of *d*-galactose residues attached to each other by a 1, 3-glycosidic linkage. This chain is terminated by one *l*-galactose residue which is attached to the rest of the chain through carbon atom 4, and is esterified at carbon atom 6 with sulphuric acid. There are probably as many as 53 galactose units to each SO_4H group. In the natural state, agar occurs as a cell wall constituent of the agarophytes, probably existing in the form of its calcium salt, or a mixture of calcium and magnesium salts.

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Contribution No. 337

TLANTIC OCEAN

by H. U. Sverdrup
and R. H. Fleming

ATLANTIC OCEAN, the name given to the vast stretch of sea dividing the continents of Europe and Africa from the new world. The term is supposedly derived from Atlantis, presumed to be a submerged continent below the present ocean.

Extent.—The Arctic basin which stretches from Bering strait across the north pole to Spitzbergen and Greenland belongs essentially to it, as in the south does the Weddell sea, south of South Georgia. The utilization of the Arctic and Antarctic circles as boundaries has neither geographical nor physical justification. The Atlantic ocean has therefore a share in both the seas of ice. From a consideration of winds, currents and temperature it is best to count the equatorial boundary of the North Atlantic at about latitude 5° N. In contrast to the South Atlantic it is very rich in islands, in variety of coastline and in land-locked seas. The latter include the Caribbean sea, the Gulf of Mexico, the Gulf of St. Lawrence, Hudson bay, Baffin bay on the west, and the Mediterranean sea, Black sea, North sea and Baltic sea on the east. Between Spitzbergen and Novaya Zemlya on the one hand and the Murmansk coast on the other lies the Barents sea; between Spitzbergen, Iceland, the Faeroes, Shetlands and Norway lies the Norwegian sea. The southern outlets from the Arctic basin are relatively narrow. Hudson strait is 48.8 mi. broad, Davis strait 146.4 mi., Denmark strait between East Greenland and Iceland 158.6 mi. and the passage between Iceland and north Scotland 518.5 mi. The total of all this is only 872.3 mi. In the South Atlantic on the other hand, between Cape Horn and South Africa, Antarctic and Atlantic meet on a 3,965 mi. front, and the South Atlantic is therefore much colder and rawer than the North Atlantic. The Atlantic is, broadly, **S**-shaped and narrow in relation to its length, with the result that writers have spoken of an Atlantic valley. From the Bering strait in the north to Coats land in the south the distance is 12,810 mi. The breadth from Newfoundland to Ireland is 2,058.75 mi. and from Çap San Roque (Brazil) to Cap Palmas only 1,769 mi. Southward from these latter it becomes broader and is bordered by very simple coasts almost without islands. Drake straits, between Cape Horn and the South Shetlands, give a passage 541 mi. wide into the Pacific. Kossinna reckons the area of the Atlantic without its dependent seas at 31,814,640 sq.mi. and with its dependent seas at 41,081,040 sq.mi. By way of comparison, one may mention that the North sea has an area of 231,660 sq.mi. Although not the most extensive of the great oceans the Atlantic has by far the largest drainage area. The "long slopes" of the continents on both sides are directed toward the Atlantic, which accordingly receives the waters of a large proportion of the great rivers of the world, including the St. Lawrence, the Mississippi, the Orinoco, the Amazon, the rivers of La Plata, the Congo, the Niger, the Loire, the Rhine, the Elbe

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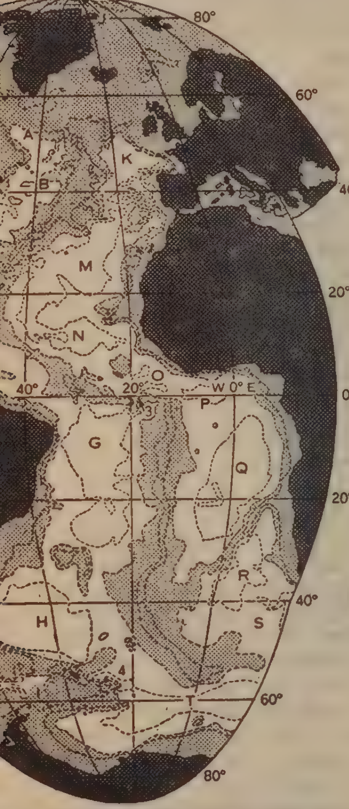

OCEAN BASINS WITH DEPTHS EXCEEDING
of Great Depths (1-4). (Based on Vaughan

	Eastern Atlantic
	J. North Polar basin
	K. West Europe basin
	L. Iberia basin
	M. Canaries basin
	N. Cape Verde basin
	O. Sierra Leone basin
	3. Romanche trench
	P. Guinea basin
	Q. Angola basin
n.	R. Cape basin
	S. Agulhas basin
	T. Atlantic-Indian Antarctic basin
	4. South Sandwich trench (8,260 m.)

AND FLEMING, "THE OCEANS" (COPYRIGHT, 1942, PREN-
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sually the result of volcanic action, we
40,540.5 sq.mi.), Fernando de Noronha
scension, St. Helena (47.4803 sq.mi.),
ouvet Islands (54° S. Lat.). Mainly
imentary foundation are the Azores,
e Verde Islands. Purely continental are
slands, the British Isles, Newfoundland,
lkland Islands, South Georgia and the
udas (lat. 30° N.) are the most north-

century. Numerous scientific expeditions, such as those of H.M.S. "Challenger" (1873–76), the German ship "Gaze (1874–76) and the U.S. surveying vessel "Blake" (1877 later), contributed to these early studies. However, the grea impetus to these investigations was the need of informatio the character of the sea bottom for the laying of transatla cables. Surveys made prior to and during the laying and repai these submarine cables led to a fairly good understanding of large-scale features of the bottom topography. Exploration the arctic and antarctic at about the beginning of the 20th tury provided information from high latitudes. The next stim to the study of the deep-sea topography arose from the inven of sonic depth finders (echo sounders) which came into ger use about 1925 (*see* OCEAN AND OCEANOGRAPHY). The genera features of the sea bottom, based on relatively few sound taken by sounding weight and wire, have been found to be oversimplified in light of the millions of echo soundings w were made after 1925. Despite the ease and rapidity with w echo soundings can be taken there are still vast areas in the A and South Atlantic that are but poorly surveyed. The install of echo sounders as standard equipment on all vessels introd an additional aid to navigation where accurate bathymetric ch are available, consequently accurate surveys of coastal wa are made out to depths of about 4,000 m. This program in Atlantic has aroused great interest in the character and orig the continental shelves and slopes and has provided informa on the history and formation of these features.

The floor of the Atlantic is divided into the eastern and we troughs by the Atlantic ridge, a tremendous elevation exte from the vicinity of Iceland to Bouvet Island in about 55° the troughs depths exceed 5,000 m., but the ridge is continuo depths less than 3,000 m. for the greater part of its length a several places extends above sea level. The islands of the Az St. Paul, Ascension, Tristan da Cunha, and Bouvet rise fron ridge. There is one small but oceanographically important in the ridge in the Romanche furrow just north of the equ where the saddle depth is between 4,500 and 4,800 m. The t verse Walfisch ridge, which extends northeast from the vic of Tristan da Cunha (37° S.) to the coast of Africa in lat 20° S., is continuous at depths of slightly more than 3,000 m divides the eastern trough. An analogous feature, the Rio G ridge, extends from the Atlantic ridge to South America in tudes 30°–35° S. but is deeper and continues only at d greater than 4,000 m. These major structures have a prono effect on the deep-water circulation and, hence, on the tem ture and other conditions at great depths.

Within the eastern and the western troughs are a numb more or less discrete basins in which depths exceed 4,000 m usually 5,000 m. In the Puerto Rico trough in the Guiana the U.S.S. "Milwaukee" obtained a sounding of 8,750 m. greatest depth thus far found in the Atlantic. A maximum of 8,260 m. has been obtained in the South Sandwich trenc arcuate structure bordering the eastern side of the South wich Islands. The basins bear geographic names.

The north polar basin and the intervening Norwegian basi separated from the open Atlantic by a ridge extending from G land to Scotland upon which Iceland and the Faeroe Island above sea level. The maximum depths in Denmark strait tween Greenland and Iceland, and over the Wyville-Tho ridge, between the Faeroes and Scotland, are only about 500 lowering of sea level of about 500 m. would impose a land from North America to Europe and completely isolate the of the polar basin from both the Atlantic and the Pacific. I north polar basin there are relatively few soundings. With mi. of the pole a Russian expedition (1937–38), which was on the ice from planes, obtained a sounding of 4,300 m. In guela current is more pronounced than its northern counterpart, the Canary current, and is characterized by lower temperatures near the coast, caused by more intense upwelling. Further south the Antarctic circumpolar current enters the Atlantic ocean through Drake passage, sending one branch, the Falkland current, a counterpart of the Labrador current, along the east coast of Argentina. The major branch of the Antarctic circumpolar current continues to the east into the Indian ocean, sending another branch to the south and feeding a large clockwise eddy in the Weddell sea.

The Deep-Sea Circulation of the Atlantic.—The deep and bottom water of the North Atlantic is, as already stated, formed by sinking of surface water between Iceland and Greenland and in the Labrador sea, from where it spreads to the south. At depths between 1,000 m. and 2,000 m. the water which flows out from the Mediterranean spreads and can be recognized by an intermediate salinity maximum. With increasing distance from the Mediterranean the salinity decreases because of mixing with other water masses, but traces of Mediterranean water are found as far south as latitude 40°S.

In the Antarctic, bottom water of temperature −0.6° C. and salinity 34.65 per mille is formed by sinking of water from the continental shelf. The temperature of this water is so low that its density is higher than that of the North Atlantic deep water. This water flows toward the north and can be traced as bottom water to 40°N. Surface water sinks at the Antarctic convergence in about latitude 50°S. and spreads to the north as low-salinity water. This Antarctic intermediate water also crosses the equator and can be traced to about 20°N. Large amounts of the Antarctic bottom water and intermediate water mix with the North Atlantic deep water, return to the south, and rise toward the surface between 50° and 60°S. latitude. In rising the deep water brings quantities of plant nutrients, phosphates and nitrates to the surface layers, and the oceanic circulation therefore accounts for the high productivity of the Antarctic waters.

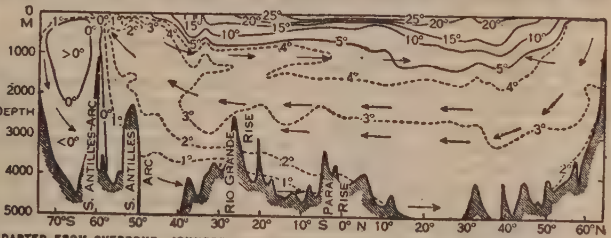

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FIG. 2.—VERTICAL SECTION SHOWING DISTRIBUTION OF TEMPERATURE IN THE WESTERN ATLANTIC OCEAN (AFTER WÜST)

The deep and bottom waters of the Atlantic are characterized by a high oxygen content because there exists a fairly rapid circulation. The waters have sunk from the surface where they became saturated with oxygen by contact with the air.

Temperatures.—The distribution of the sea-surface temperature is closely related to the character of the currents. The waters of the north equatorial currents spread to the north and to the south when reaching the east coasts of North and South America and, correspondingly, the region of high-surface temperature is very wide off the American east coasts but is narrow off the African coast where the Canary current and the Benguela current carry cold water toward the equator. Therefore, in latitudes about 10°S. to 30°S. and 10°N. to 30°N. the sea surface is warmer off the eastern coast than off the western, but poleward of 30° this feature is reversed. This reversal is barely evident in the South Atlantic where the Falkland current carries cold water up to about latitude 30°S. (in August to 25°S.) but is very conspicuous in the North Atlantic. There the Labrador current brings cold water to latitude 40°N., whereas the extreme branches of the Gulf stream system carry warm water along the coast of Norway where ports remain ice-free even in latitude 71°N. The contrast between the South and the North Atlantic is related to the surface currents which in turn reflect the action of the prevailing winds and the effect of the shape of the coasts. Where the Falkland current meets the Brazil current and where the Labrador current meets the Gulf stream the surface temperature changes rapidly on a very short distance. The change is particularly striking when passing from the Gulf stream to the Labrador current ("the cold wall").

In the tropics the surface temperature is controlled by climatological factors to such an extent that it is nearly uniform, and differences related to currents do not appear. Such differences are very marked, however, at a depth of about 200 m., where the latitude 6°–7°N.

Contribution No. 338

OLOURS OF ANIMALS

by Francis B. Sumner
and Denis L. Fox

OLOURS OF ANIMALS. This is a subject at once of siderable aesthetic appeal and of high scientific interest. Many he most beautifully coloured objects in nature are animals or derived from animals. On the scientific side, there are ques- ns of the physical and chemical basis of animal coloration, and ts value, if any, in the economy of the organism. Colour, in- d, has figured importantly in nearly every branch of biology: biochemistry, physiology, pathology, histology, taxonomy and etics, both of animals and plants; as well as in psychology, h human and comparative. In general, the colours of animals the result of two chief causes: (a) the minute structure of terials, chiefly ones on the body surface (the so-called physical structural colours); (b) the presence of substances which sess colour independently of the arrangement of their particles emical or pigmental colours).

STRUCTURAL COLOURS

he physical principles of total reflection, interference, scatter- and to some extent, diffraction, all familiar in the inanimate ld, are encountered also among tissues and tissue products of mals.

otal reflection of light, imparting whiteness to animal struc- es, often arises from the separation of finely divided structural terials by air spaces in the way that whiteness is conferred n snow. Examples of this are seen in the whiteness of feathers, and hair, and in the wings of certain butterflies. Secretions deposits in animal tissues may also contribute to the white- s of total scattered reflection, examples being colloidally dis- sed fatty or lipoid materials, calcium carbonate in the skele- s of numerous molluscs, crustaceans, corals, echinoderms and tozoans, silica in sponges, proteinaceous materials in various ous membranes, deposits of white pterins in the wings of pierid other butterflies and silvery aggregates of crystalline guanine other purine materials (*q.v.* infra) in numerous invertebrates in fishes' scales.

Disintegration of white light into its spectral components oc- s in animal structures chiefly through interference, wherein the ident light penetrates and is reflected back through successive n-layered films or laminae to give striking iridescence, even in use light. Iridescent interference colours are very common in tain animal structures, including the wing scales of *Morpho* other butterflies, the brilliant rainbow hues observed in the thers of humming-birds, peacocks, pheasants, etc., in the wing vers of many beetles, the outer skin of reptiles, nacreous sur- es of Pearls and in molluscan shells and the setae or bristles numerous marine worms (*e.g., Aphrodite*). The brilliant lustre human or other mammalian hair and its iridescent appearance direct sunlight is due to the same phenomenon, the light being lected in its disintegrated components by minute transparent les which surround each individual hair. Pure prismatic refrac- n of light in animals is probably very rare, and limited to cases erein direct beams of light encounter certain microcrystalline posits. Diffraction by natural gratings or regular fine parallel iations is not uncommon among certain insects, but is percep- le only when a direct beam of light strikes such structures at angle. Studies with the electron microscope have confirmed presence of such natural diffraction gratings in some insects, tably the elytra or wing coverings of certain iridescent beetles.

Very common in animals is the display of blue colours, arising t from blue pigments but from scattering of reflected light by ely dispersed colloidal systems, lying over layers of dark me- in deposits. Examples of these structural blues are numerous. ue eyes, wherein the turbid stroma of the iris overlies the dark mbrane or uvea, may be simulated by placing disks of agar gel or dried collodion film upon a black surface. The blue skin about the head and neck of the cassowary or on the face and buttocks of certain primates results from the scattering of light by colloidally dispersed materials in the skin, overlying an absorbing layer of melanin pigment beneath. The gorgeous blues of the integument of various reptiles and fishes could be added to the many other examples of structural blue.

Two types of structural coloration may be combined, *e.g.*, diffraction and interference. In many other cases, the two underlying causes, structural and pigmental, are superimposed. Most of the greens found in fishes, amphibia and reptiles do not really depend upon the presence of a green pigment, but result from the association, within the tissues, of black and yellow. The otherwise sombre colours of black or brown pigment, when suitably reinforced structurally, may give rise to a resplendent glitter.

THE CHEMISTRY AND PHYSIOLOGY OF ANIMAL PIGMENTS

The visible range of light is selectively affected by reflection from or transmission through materials, only if the latter contain structural units whose size or vibrational frequencies lie between 3000Å and 7000Å. Those physical structures in the biological world which may disintegrate white light into spectra have already been considered; namely, very thin, finely spaced laminations, or closely placed ridges or striations, or very fine, colloidally dispersed micelles which scatter incident light, reflecting only the blue rays, these being the most refrangible.

This brings the discussion to a consideration of the chemical pigmentary compounds which, irrespective of physical orientation, selectively absorb a part of the light and reflect or transmit the unaffected fraction. Since the word pigment is based upon a Latin verb meaning "to paint," its original significance obviously had to do with the use of colouring matters for human ends. Those coloured substances were called pigments which were used as such. In transferring the term to the living world, this functional connotation has for some reason been abandoned. Any coloured substance which can be extracted from an animal or plant, regardless of its function, forthwith becomes a pigment. Owing to long-established precedent, this somewhat illogical use of the term will be employed in the present article, though a more recent word, biochrome, will be used as an alternative.

The colour of a compound depends upon the selective absorption of incident light within definite wave lengths, the unabsorbed residue being reflected or transmitted to the eye. This capacity to absorb visible light is due, in turn, to varying kinds and degrees of chemical unsaturation, or unfulfilled valencies, located in so-called chromophores (colour-carrying groups) within the molecule (*see* DYES). These areas of special molecular activity arise from reduction in the relative speed or frequency of motion on the part of one or more pairs of the compound's many rapidly vibrating electrons. Indeed, sufficient modification in the speed of electronic vibration imparts to the entire molecule a degree of special vibratory motion or chemical resonance. And this phenomenon, in the modern view, is the basis of colour manifestation.

Consider, as a crude analogy, a long horizontal cord or chain (representing a chemical compound), suspended just above or below the view of an observer looking through a long, narrow slit placed parallel to it (representing the visible spectrum of light). If, at certain points or links of the chain, threads be attached, and if these threads be given rhythmic jerks by an operator, the whole length of the chain will be thrown into a series of waves,

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As a result, portions of the chain will come into view through the slit, at heights and intervals depending upon the intensity and frequency of the pulses imparted to the chain at the various points of focus. Obviously, rapid, gentle pulls at a number of points of the chain would give the observer a resonance pattern of many rapid undulations of minor calibre, while more vigorous jerks at one or two points would reveal through the slit slower, higher wave pulses, and so on.

A molecular chainlike compound in a resonating condition absorbs, by internal interference or frictional forces, that critical fraction of incident light whose wave length corresponds with the resonance-frequency peculiar to the compound. The absorbed light is converted into heat, and the residual portion which emerges is of a complementary colour. Thus, if the resonance involves short, rapid waves (corresponding with rapid undulations in the analogous chain seen through a slit) the shortest visible light waves will be absorbed, *i.e.*, those of the violet and blue spectral region, and the compound will appear yellow. Red substances, having slightly longer resonance values, similarly extinguish light in the blue and green, while blue or green compounds result from cancellation of light in the red or orange realm. Black substances absorb all light equally and completely.

The colours of most chemical compounds are not of spectral purity, but include all of the visible light excepting the absorbed fraction; the colour of a molecule depends upon the dominant wave length, or that of maximum transmission.

There is good ground for the view that colour and chemical reactivity, and hence the potential metabolic value of a pigment to an organism, are parallel expressions of the same underlying molecular property of unsaturation. This is a reason for the careful consideration of the physicochemical attributes of biochromes and for continued researches regarding their metabolic position in the animal organism.

The more important biochromes of animals may be grouped into classes whose molecules are without combined nitrogen and others which contain this element.

Of the non-nitrogenous pigments, by far the most important, the most conspicuous and the most widely distributed are the carotenoids or polyenes. Indeed these are among the most widely distributed of all biochromes. Chromolipoids, naphthoquinones, anthraquinones and flavones represent other nitrogen-free pigments which occur in animals, but these are limited in distribution, and but little is known of their physiological attributes.

In the nitrogenous group are several pigments of very diverse chemical nature and metabolic position. The tetrapyrrolic pigments include both the porphyrin class, present in the blood of many animals, and the bile pigments, occurring in many secretions and excretory products; the dark melanins occur in skin, hair and other parts, and represent metabolic end-products. Several purines, while usually white or silvery in appearance, are included as biochromes or pigments because they contribute to the total colour of numerous lower animals; similarly the pterins, which are derivatives of pyrimidine, are frequently white, but may often be yellow in colour; the lyochromes or flavines, detectable in the tissues of all or nearly all living organisms, are identified with certain important biocatalysts; finally the indole derivatives, which are somewhat limited in any conspicuous manifestation are, like the melanins, purines and pterins, end-products of metabolism.

In the following treatment are outlined the chemical configuration, colour, source and metabolic features, insofar as the latter are known, of some representative animal biochromes comprised in these groups. Lastly, a few of many miscellaneous coloured compounds will be considered, whose chemical structure is yet imperfectly known.

Carotenoids (Fig. 1).—These red, orange, or yellow pigments, whose numbers of known compounds is constantly increasing, are of such wide distribution throughout the living world as to be nearly universal. The carotenoids are insoluble in water, but may be readily dissolved in alcohol, ether, chloroform and the various other organic fat-solvents. They show pronounced and consist crystalline habits, and in solution, exhibit usually two, o three, but in some cases only a single absorption band, cha teristically in the violet to blue, sometimes extending into green region of the visible spectrum. They are readily bleac by light and by exposure to atmospheric oxygen, are unstable in the presence of mineral acids, their chloroform solutions ing dark blue coloration upon treatment with concentrated phuric acid.

The chromophore grouping, or chemical configuration respo ble for the colour, is the long chain of alternating points of saturation, or so-called conjugated double-bond structure, re sented in the formula given for β-carotene. A number of c tenoid hydrocarbons share this constitutional formula C_{40} Carotenes and xanthophylls ($C_{40}H_{56}O_n$. . .) occur together many organisms, and may be separated on the basis of their p erential solubilities in certain solvents, and by differential ads tion from solution upon packed columns of relatively inert p ders, such as chalk, sugar, alumina, magnesium oxide, etc., whe the pigments appear as distinct coloured bands or zones. T may then be resolved into individual components by chemical traction of each mechanically isolated zone.

These pigments occur in plant organisms ranging from simplest types, *i.e.*, bacteria, fungi and algae, to the most hi evolved flowering plants. Animals from simple Protozoa to highest mammals, including man, contain carotenoids, altho the tissues, and notably the blood sera of a number of mamm are almost or entirely devoid of these pigments. The liver some of such species often yield carotenoids, and it is known the lives of these animals depend upon a supply of caroten its metabolic derivative, vitamin A. Carotenoids are relati more concentrated in ovaries or eggs, some testes, liver (or li like analogue in invertebrates), skin, eyes and milk. Outstan common examples of visible carotenoid pigmentation are in legs, body-fat and eggs of domestic poultry, the bright red, or and yellow feathers of many birds, similarly coloured wing co of numerous insects, and the milk-fat of cattle. In some ani a high degree of specificity exists for the absorption of either hydrocarbon (carotene) class or the oxygenated (alcoholi xanthophyllic) type of carotenoid. The horse, for example, sorbs through the intestine only carotenes, from green food taining an ample supply of both kinds of carotenoid. The he the other hand, stores only members of the xanthophyll c many fishes and marine invertebrates likewise store only xa phyllic carotenoids, rejecting in the faeces or otherwise to disposing of the carotenes. Other animals, including the frog man, assimilate and store both classes in depot-fat.

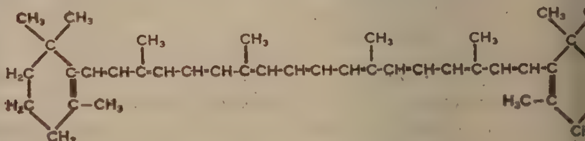
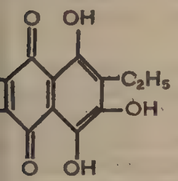


FIG. 1.—β-CAROTENE

Strikingly beautiful displays of carotenoids are encountere the skins of numerous amphibians, notably among salaman many species of fish, and countless marine invertebrates, cially among the echinoderms (sea stars and brittle stars), luscs, ascidians (sea squirts), crustaceans, the tissues of co terates including many anemones and corals and many speci marine worms. The gorgeous blue and green, some gray or ch late tones, violet and near-black pigments of certain crustac naked molluscs and sea stars are in many instances due to tenoids in chemical conjugation with protein. Denaturation o protein by immersion of the specimen in boiling water or in hol unmasks the bright red colour of the carotenoid invo Hence the familiar red colour of boiled lobsters. Marine ani commonly derive their rich supplies of carotenoids directly o directly from the countless microscopic plants. Even carnivo s and flesh- or mud-eating invertebrates from the great un- ed depths frequently exhibit rich pigmentation, derived ulti- ly from supplies of carotenoids long since generated in lighted rs and buried in the ocean floor.

yellow condition of the skin, known as xanthosis, carotenae- or artificial jaundice may follow excessive eating of caro- d-rich foods such as carrots or oranges; the condition, less non in adults than in children, is unaccompanied by patho- al symptoms and disappears when excessive supplies of enoids are withheld from the diet.

ns and fish mobilize body carotenoids in their eggs during g (or spawning) season, with an obvious diminution of the w biochrome from its former conspicuous position in the Males of these species may continue to exhibit the pigmen- n, however, those of many species showing an actual enrich- of the colour during the reproductive period.



2.—ECHINOCHROME

aphthoquinones (Fig. 2).—These compounds, occurring in y plants, are yellow, orange, red or purple in colour, soluble rious organic solvents, and have found considerable use as for fabrics. Their occurrence in any conspicuous degree g animals seems to be limited to the echinoids (sea urchins sand dollars) whose spines, shell and thin skin are consequently rendered distinctly red, purple and in some instances green by echinochromes. Red aggregates of this class of biochrome are found in the body fluid, inner lining of the shell, and in the lining of the alimentary tract of numerous species of echinoid, and some members bear the dye also in distinct masses within the jelly surrounding the eggs.

Like other quinones, echinochromes are y oxidizing, and lose their colour when treated with chem- reducing agents. They assume different colours also ac- ng to the acidity or alkalinity of their surroundings. The le or red colour of sea urchins is consistent with the faint- kaline condition of the tissues and calcareous shell. The aemorrhagic factor, vitamin K, is a naphthoquinone of w colour. Other naphthoquinones are reported to possess nin K potency as well. Echinochrome has been assigned a as respiratory stimulant for sea urchin eggs. It is believed ome investigators to cause stimulation of the spermatozoa rtain species of sea urchins and to attract the latter to the

e diverse coloration of spines, tests and other structures of in species of sea urchin are attributable to the presence of ures of echinochrome and a chemical homologue, spino- ne, in various proportions. Studies of crystalline melting , absorption spectrum and other properties indicate that a ber of different echinochromes exist.

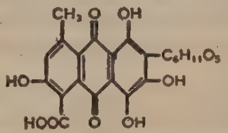


FIG. 3.—CARMINIC ACID

nthraquinones (Fig. 3).—A large number of brilliantly red compounds which have found application as dyes and chemical in- ors of acidity or alkalinity are in- d in this group. Like the naphtho- nes, with which they share a common nophoric structure, they may be ically reduced by certain reagents. inic acid is the red biochrome consti- g about 10% of the product cochineal, obtained from the le scale insect *Coccus cacti,* found in Mexico and Central Amer- The pigment imparts permanent red colours to mordanted wool silk. Kermesic acid from another scale insect, *Coccus ilicis,* llow-red in water, and violet-red in acid solutions; it is em- d as a dye as is carminic acid, from which its chemical struc- differs in only a minor way. Laccaic acid is isolated from ye or lac-lac, the solid exudation of East Indian lac insects, *us laccae.* This scarlet or carmine-red dye possesses a con- tion similar to that of the above-named compounds. While e conspicuous anthraquinones are beyond doubt derived by scale insects from the plants upon which they feed, no information is yet available relative to their metabolic path or possible physiological role.

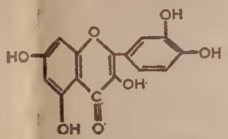


FIG. 4.—QUERCITIN

Flavones (Fig. 4).—Considerable chemical study has been devoted to this large group of coloured compounds which occur in a wide variety of plants and in a few insects which feed upon such plants and assimilate some of the pigment. These compounds impart yellow colours to flowers and other plant parts. The chemical properties of a yellow biochrome isolated from the wings of a butterfly, *Melangaria galatea,* correspond closely with those of the plant pigment quercitin. The chemically related anthocyanins, which are the red, violet and blue compounds often seen in blossoms, fruit and leaves of plants, are occasionally encountered in certain dipterous and hemipterous insects and their larvae, commonly in the albuminoid inclusions of fat cells. None of these classes of biochromes has been shown to fulfill particular physiological functions in animals, although they are believed to be involved in certain biochemical oxidations in the plants which synthesize them.

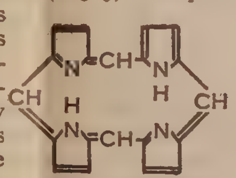


FIG. 5.—PORPHIN

Tetrapyrroles.—*A. Porphyrin Compounds (Fig. 5).*—Porphin is the parent compound of the whole class of nitrogenous water-soluble biochromes under discussion in this subsection. Bearing side chains of various lengths composed of carbon, hydrogen, and frequently oxygen, linked to different carbon atoms of the four pyrrole nuclei, porphyrins are represented in the green photosynthetic chlorophylls of plants and in animal haemoglobins. Haemoglobins are conjugation products between a protein body, globin, whose composition varies with the species, and a porphyrin, haem, $C_{34}H_{32}O_4N_4Fe$, whose pyrrolic nitrogen atoms are attached to an atom of iron. Haemoglobins are present in the red blood cells of mammals, birds, reptiles, amphibians and fishes, and in the circulatory fluids of numerous invertebrates, notably among the worms, and in scattered members of the arthropod, echinoderm and molluscan phyla. Having the unique capacity to combine with atmospheric oxygen in lungs, gills or other respiratory surfaces of the body, and to again release it among tissues of lower oxygen content, haemoglobins thus serve as respiratory catalysts. These compounds are responsible for the pink to red colours observed in combs and wattles of birds and the skin of man and other primates, notably that covering portions of the face, buttocks and genital regions of baboons.

Other biochromes chemically allied to the haem compounds are cytochrome, the red oxidation enzyme which occurs in minute concentrations in nearly all cells; catalase, an enzyme of similar distribution which accelerates the breakdown of hydrogen peroxide; pinnaglobin, a brown compound which serves as a respiratory aid in the mollusc *Pinna squamosa;* chlorocruorin is a green pigment which plays a similar role in the blood of tube-building annelid worms; a red compound, helicorubin, is encountered in the liver and gut of some snails, and actineohaematin is responsible for some of the beautiful red colours of sea anemones. The physiological functions, if any, of the latter two pigments have not been clarified.

Numerous porphyrins are present in secretory and excretory products of animals, and others may be extracted from ancient deposits such as coal, petroleum and mud from long-buried strata of the ocean floor. Many porphyrins are readily isolated, crystallized and identifiable by their manifestation of spectral absorption bands at given positions in the visible spectrum.

Oöporphyrin is responsible for the red flecks upon the eggshells of the plover. The shell of the emu egg is coloured by a biliverdin, found also in the skeleton of the blue coral *Heliopora caerulea.* The remarkable turaco bird excretes a copper salt of uroporphyrin in its quill-feathers. This red pigment, known as turacin, is readily leached out of the feathers by water containing traces of alkali. A similarly occurring green porphyrin in feathers of the turaco is turacoverdin. Certain molluscs excrete coloured porphyrins in the material of their shells. Bonelline, obtained from alcoholic extracts of the worm *Bonellia viridis,* is an alkaline biochrome giving blue solutions in acids; its properties have led to its inclusion among the pyrrole pigments. The chemical structure of so-called enterochlorophyll found in the liver of numerous molluscs, crustaceans and even in the digestive gland of carnivorous sea stars, has not been determined.

B. Bile Pigments (Fig. 6).—Among the metabolic breakdown products of haem or allied biochromes is a series of yellow, green, red or brown nonmetallic tetrapyrroles arranged in open-chained molecules typified by the simplest synthetic member bilane. Small quantities of the red compound, bilirubin ($C_{33}H_{36}O_4N_6$), its green oxidation-product biliverdin, and various other chemically homologous products occur in normal tissues, and may be conspicuous in excretory and secretory products under certain pathological circumstances.

Various compounds of the bile-pigment series are encountered in birds and in lower animals. Oöcyan, closely related to bilirubin, imparts a blue or blue-green colour to the eggshells of numerous birds. Pterobilin is a blue pigment observed in many pierid butterflies' wings, and other insects and their larvae exhibit or excrete allied compounds. The liverlike organs of numerous invertebrates seem to lack bile pigments, containing instead porphyrin compounds, exemplified by helicorubin in some molluscs and crustaceans. Certain leeches, nourished by the blood of vertebrates, contain blue-green, red or brown bile pigments in their blood, probably as a result of the breakdown of ingested haemoglobin.

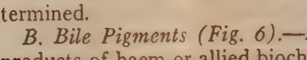


FIG. 6.—BILANE

The sea anemone *Actinia equina* carries beneath the outer skin and at the base of the foot a green pigment believed to be biliverdin which occurs also in other anemones. The dark red or violet biochrome encountered in the strikingly coloured anemone *Calliactis parasitica* has been termed calliactine. It is a natural indicator, being yellow-brown in acid, becoming golden to orange in less acidic solutions, and changing to blue, violet and finally red in alkalis. It can be crystallized in a pure state as blue-violet rosettes of needles which, when dissolved in dilute aqueous solutions, exhibit characteristic absorption bands, according to the acidity or alkalinity of the solvent. Calliactine is easily and reversibly oxidized and reduced, which fact suggests its possible function in oxidative metabolism. Certain molluscs display colours in their tissues or shells which are attributable to the presence of biochromes of the bile-pigment class. Examples are the red compound, rufine, in the snail *Arion rufus,* another red colouring matter in the shells of abalones and some turban shells, called rufescine, and a blue-green one in another species of abalone. The purple colour of the offensive, mucous-laden ink of the sea slug *Aplysia* (*Tethys*) is due to a pigment, aplysiopurpurin, closely
similar to mesobiliviolin, conjugated with protein material as
other pigments, including mesobilirhodin and urobilin which
company it. Numerous fishes among the Belonidae and Cotti
bear strikingly blue-green coloured skeletons. The green pigm
in the bones and scales of the garfish *Belone belone* is a bile
ment, related to biliverdin.

Melanins (Fig. 7).—Dark colours, indicating the presence
melanin pigment, are observed in mammalian hair and eyes an
the skin and scales of numerous fishes and reptiles, the ink
cephalopods, various tissues of numerous other invertebrates
in skin-moles of man and black tumorous growths of various m
mals. Melanin, an end-product of metabolism, is formed as a
sult of serial oxidation and polymerization of tyrosine or sim
phenolic compounds. This oxidation by dissolved atmosph
oxygen is catalyzed by an enzyme tyrosinase. Chemically re
sible yellow, orange or red stages in the successive oxidation
followed, if uninterrupted, by a final intensely black prod
Some white or albino animals may lack the enzyme tyrosinas
its active form, or they may have means of excluding the enz
and the substrate, tyrosine, from each other. Completely whit
red variants of the anemone *Metridium senile*, for example,
to develop melanin in their tissues as do brown variants of t
species. But upon death, or upon grinding of the tissues of
an albino animal, the macerated material blackens rapidly
the formation of melanin.

Pale yellow, tawny, buff, red and brown colours of hair are
to melanin in intermediary phases of formation or in relati
finely divided condition. The importance of dark, light-absor
sublayers of melanin in intensifying structural blues or irides
colours has been mentioned. Genetic or photically induced m
nization of human skin serves an important function in prote
underlying tissues from injurious sunrays.

Certain fishes exhibit a striking ability to synthesize and
in their skins more melanin when kept on dark backgrounds
do members of the same species maintained in pale surround
all of the specimens receiving the same amount of incident
from above. (See *Adaptive Colour Change*, below.)

Black or brown melanins or melanoproteins are to be obse
in numerous invertebrate animals in addition to those menti
Certain of the worms, numerous crustaceans and many class
molluscs exhibit melanism in the integument. The red inter
ate compound, formed during the transformation of tyrosi
melanin (*see* formula) is hallachrome, which is encountered
in the marine worm *Halla parthenopaea.* It is green in
beyond pH 8.3. This biochrome may be reversibly oxidized
reduced; it is said to stimulate increased respiration in ce
invertebrate eggs. Its original precursor may be either tyr
or tryptophane. Red or yellow uranidines, found in spo
corals, medusae, holothurians (sea-cucumbers) annelid worm
tunicates, are believed to be chemically related to the mel
Urochrome, the principal yellow pigment of urine, is c
ered to be a modified melanin. In certain diseases, melanin
cursors cause urine to darken as oxidation occurs on sta
(melanuria, alkaptonuria).

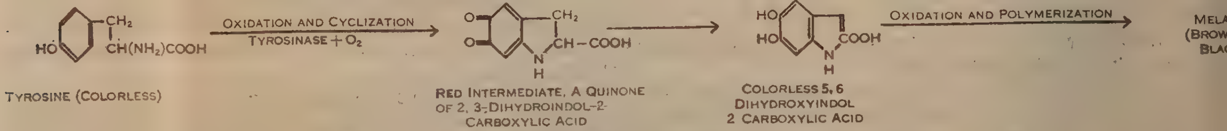
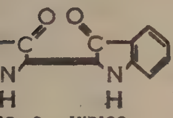

CH₂
HO
CH(NH₂)COOH
OXIDATION AND CYCLIZATION
TYROSINASE + O₂
O
O
CH₂
CH—COOH
N
H
HO
HO
COOH
N
H
OXIDATION AND POLYMERIZATION
MELA
(BROW
BLA
TYROSINE (COLORLESS)
RED INTERMEDIATE, A QUINONE OF 2, 3-DIHYDROINDOL-2-CARBOXYLIC ACID
COLORLESS 5, 6 DIHYDROXYINDOL 2 CARBOXYLIC ACID

FIG. 7.—TYROSINE (COLOURLESS) CONVERTED TO MELANIN PIGMENT

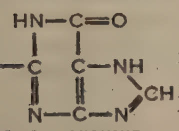
dole Derivatives (Fig. 8).—Certain similarities between olic features applying to the two amino acids, tyrosine and ophane, lead next to a consideration of the biochromes de- from the latter compound. Like melanins, the indole atives are excretory products of certain animals, but in con- to melanins, their distribution as pigmentary compounds latively limited. Unlike the dark, sombre melanins, too, erous indole compounds are of striking red, green, blue or e colours. Indigo occurs as a glucoside in many plants of the East Indies, Africa and South America. It has long used as a blue dye. While the pigment itself does not occur althy animals, certain chemical derivatives of it are found in tory and excretory products.


IG. 8.—INDIGO

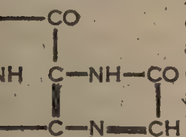
Hallachrome, the red pigment in the epidermis of a marine worm, has been discussed. This compound, as well as the chromogen of human melanuria, which is probably a derivative of 5,6-dehydroxy indole, may be generated from the breakdown of either of the common amino acids, ine or tryptophane.

rian purple, a purple of the ancients, is 6–6′–dibromindigo ned by the irradiation of a glandular secretion of several es of gastropod molluscs of the genera *Murex* and *Purpura*. e this red-violet dye has long been employed commercially rtain countries, its physiological use to the animals producing obscure. In all probability it is an excretory product.

rines (Fig. 9).—The members of the purine class of comds are hardly to be considered as true pigments, since they usually white crystals. But they often contribute to the r scheme of lower vertebrates and invertebrates, hence their sion in the section. The position of purines as excretory ucts is amply illustrated by the large amounts of guanine in xcrement of birds, and of uric acid in that of reptiles. Uric has also been found in the yellow sheets of mucous excreted ea anemones. The brilliant whiteness of some anemones, bly the white variant of *Metridium senile*, results partly from ocrystalline deposits of uric acid in the tissues. These crystalline aggregates are especially noticeable in the mesenteries. Other purines, such as xanthine, have been reported as occurring in the wings of pierid butterflies. Mention has already been made of the notable deposition of guanine crystals in the leucophores or iridocytes of fishes, contributing iteness, or often a brilliant silvery appearance to extensive s of the skin. Note has also been made of the ability of some s to vary the quantities of deposited guanine in proportion to ightness of the background upon which they are living. Purine pounds constitute part of the complex nucleic acids which nd in the nuclear material of all cells; it is therefore pre- ed that they play an indispensable part in cell metabolism. purine compound hypoxanthine exercises a specific stimulat- nd accelerating effect upon the growth of embryonic tissues ne chick.


G. 9.—GUANINE

terins (Fig. 10).—Closely related to the purines, and for- y classed among them, are the so-called pterins, which derive name from their notable appearance and primary chemical isolation from the wings of certain species of butterflies, wherein they are sometimes accompanied by purines. Pterins are encountered as white, yellow, orange or red granules in association with the wing material, and contribute the yellow colour to the body-integument of numerous wasps. The pterins are soluble in aqueous solu- s, often more so in the presence of ammonia, and insoluble in usual organic solvents. Leucopterin is a white compound ob- ed from *Pieris brassicae* and *P. napi*, and has been found ac- panied by other pterins in other species. Xanthopterin is a yellow biochrome responsible for the yellow colour in the wings of *Gonepterix rhamni* and other butterflies, and in the abdominal skin of wasps (*Vespa* spp.). It occurs also in human urine, and therefore is often called uropterin. This compound has been found to be effective in preventing nutritional anaemia in rats and in young salmon. No physiological roles other than their excretory character have been recognized in the other pterins which occur in Lepidoptera; the colourless compounds guanopterin and mesopterin may be accompanied by chrysopterin, an orange compound, or by a red homologue erythropterin; the latter imparts conspicuous red colours to the wings of several species. The red biochrome in the eyes of the fruit fly, *Drosophila melanogaster*, of great interest and usefulness to geneticists, is believed to be related to the pterin class.


10.—XANTHOPTERIN

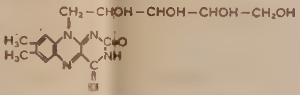


FIG. 11.—LACTOFLAVIN

Lyochromes or Flavines (Fig. 11).—This class of yellow, greenly fluorescent, water-soluble biochromes is very widely distributed in plant and animal tissues, although their presence in very small amounts renders their colour unappreciable in animals save following appropriate chemical extraction. Although synthesized by bacteria, yeasts and the green plants, the lyochromes, notably lactoflavine (riboflavine), which is identical with vitamin B_2, is not manufactured by animals, which thus depend upon plant material for their ultimate supply of this important factor. Lactoflavine, conjugated with a protein, has been shown to be identical with the yellow oxidizing enzyme described by O. Warburg and W. Christian in 1932. The enzyme is capable of combining with molecular oxygen, whereupon the yellow colour develops. It may then release this element for intracellular oxidation processes, with simultaneous loss of colour. The colour is again restored by fresh supplies of oxygen. Blood, milk, eggs, liver, kidney and muscle contain appreciable quantities of the biochromic catalyst. Physiologically, a nutritional lack in the supply of lactoflavine leads to impairment of cellular respiration, retardation in growth of young mammals, and to cataract in the eyes of mice, chickens and monkeys. The compound is not stored in quantity and is a normal excretory product. This flavine has been encountered in somewhat concentrated amounts in the Malpighian tubules of insects, which obtain it from fresh vegetable material. The larvae of mosquitoes responsible for carrying yellow fever fail to develop normally, or to complete their metamorphosis if deprived of flavine and purine.

MISCELLANEOUS BIOCHROMES

There are many animal colouring matters whose constitutions remain unknown. Of these, only a few of the more conspicuous examples will be mentioned.

Chromolipoids are a class of yellowish, reddish or brown fat-soluble biochromes often encountered in the fat-droplets of eggs and other cells and in other lipoid-rich tissues. These compounds have often been mistaken for both melanins and carotenoids. They are believed to be derived from partially oxidized fatty acids, phospholipids or other lipoid compounds, perhaps in ways similar to those in which commercial fats may gradually become discoloured on being heated or after long standing in air.

Haemocyanin is the respiratory catalyst encountered in the plasma of molluscan and crustacean blood. It is colourless in the reduced condition, but assumes a blue colour upon exposure to oxygen, with which it combines. During the circulation of the blood, the oxygen carried in combination with haemocyanin is released to the tissues requiring it. Chemically, haemocyanin is composed of a large protein complex bound to copper, whose presence is responsible for the blue colour of the oxidized molecule.

Haemerythrin is an iron-containing proteinaceous biochrome present in the blood of gephyrean worms, serving there as a reversible oxygen carrier just as do haemoglobin, chlorocruorin and haemocyanin. The blood containing haemerythrin is pale when in the reduced condition, but red or reddish-brown when oxygenated.

Vanadium chromogen occurs in blue, green or orange aggregates within the corpuscles of the blood of tunicates. Chemically this unique biochrome series represents protein combined with vanadium in various stages of oxidation. Owing to the presence of rather remarkable amounts of dilute sulphuric acid in the corpuscles of these animals, the biochrome readily yields its combined oxygen to surrounding tissues.

Numerous coelenterates exhibit brilliant pigmentation, the chemical nature of which is as yet very imperfectly known. For example, the lasting red pigment in skeletons of the corals *Corallium rubrum* and *Tubipora musica*, and the red, orange and yellow colouring matters of many other alcyonarian skeletons are chemically obscure.

USES OF COLOURS TO ANIMALS

Under this head are two distinct classes of problems: (a) the value of the colours as such to the organisms possessing them; (b) the value to the organisms of the substances giving rise to these colours. The one case has to do with the value of appearance to the animal, regardless of how this is brought about; the other case with the utilization for one or another function of substances which happen to be coloured. Any discussion of these matters must include black and white pigments among the substances influencing colour. The second of these classes of problems has already received some attention, in connection with the chemistry and physiology of animal pigments. As there stated, some of these coloured substances have a high physiological importance to the organism, in relation to their respiratory function, or as products of fundamental metabolic processes.

One service which the pigments or biochromes render to the organism is the protection of certain tissues, notably the retina and central nervous system, from the rays of the sun. Here should be mentioned, too, the dense layer of pigment cells (chromatophores) which lines the peritoneum of many fishes and some other vertebrates. The function of such a layer is not certain, though it may well relate to the protection of the viscera from sunlight. The cephalopod molluscs, when disturbed, discharge a dense cloud of black ink (melanin) into the water. This is commonly interpreted as a smoke screen, serving to baffle pursuers.

As already stated, white in the animal kingdom is sometimes due to special white substances (guanine, etc.) deposited in the tissues; in other cases to the mere lack of coloured substances, the place of these being taken by air. This is notably true of the hair of white mammals and the plumage of white birds. The colours of arctic animals belong in a later section of this discussion, since the importance of these animals' appearance is probably a real factor in the evolution of their colour. However, the suggestion has often been made, and with some plausibility, that a white plumage or pelage is of value in retarding the radiation of heat. Consistent with this view is the fact that some of these animals lay aside their white garb and assume a darker one during the summer. It is possible that in these cases both factors, the concealing and the heat-conserving one, are operative.

Concealing Coloration (Procryptic and Anticryptic Coloration).—The optical principles which became familiar to the world after World War I, under the name of camouflage, have probably been utilized in the animal kingdom from the time that predators began to rely upon their sight in hunting their prey. Naturalists were doubtless early impressed by the widespread existence of protective coloration, since any collector of living specimens, vertebrate or invertebrate, is constantly balked in his search for objects which, as he may know, lie before his very eyes. The prevailing sandy hue of desert animals, and the frequency of green in animals inhabiting trees are familiar to the field naturalist. Less familiar are special cases where extensive areas of black, volcanic rock in the desert have called forth appropriate darkening effects in animals which, in
surrounding areas, display the prevailing pale hue. Such f
serve to refute any general explanation of the pallor of de
animals as due either to the direct effects of solar radiation o
the animal's need of reflecting this from its surface. The
portance of the principle of protective coloration as a facto
evolution was fully recognized by Darwin and some of his
temporaries, and it soon became one of the standard exam
of the working of natural selection. It required consider
sophistication for zoologists of a later generation to reject
plain testimony of their senses and to dismiss the protective col
tion theory as unfounded. However, more extensive knowle
including experimental evidence that protective coloration
in reality protect, led to a return, more nearly, to the view
Darwin and his followers. If one had to do, in these cases, me
with a general resemblance in colour between the organism
its more familiar environment, one might seek for some di
physical or chemical influence of the latter upon the former
has been done by more than one critic of natural select
But one frequently has to do with a striking resemblanc
pattern, *i.e.*, in the distribution of pigment upon the anin
surface such as frequently to match in detail features of
more habitual background which the animal occupies. Som
the most striking cases of this sort are to be found in the sp
fauna of the *Sargassum* or floating seaweed of certain areas o
tropical Atlantic. Here are animals, belonging to several diffe
subdivisions of the animal kingdom, not only displaying the
ours of the seaweed itself, carefully reproduced, but even c
ing the white patches of the encrusting bryozoan by which th
conspicuously mottled. In certain of these organisms, too,
skin is extended into long fleshy appendages which closely im
similar structures upon the fronds of the weed. It is ha
likely that these resemblances would be attributed to chanc
anyone who had actually seen these organisms together u
natural conditions. Furthermore, any naturalist with much
experience knows that correspondences of this sort are far
being rare or exceptional. Specific resemblances to parti
natural objects, *e.g.*, to leaves, sticks or stones, or to other
mals, occur with convincing frequency, while even the s
which seems to mimic the excrement of birds is difficult t
terpret in any other terms. We must add to these resembl
in colour and structure the frequent occurrence of approp
instincts controlling the attitude assumed by the animal, o
posing quiescence or movements of a sort calculated to de
the enemy. The walking stick, for example, would not be
protected by its form, unless it also behaved like a stick
reduced its movements to a minimum.

Another class of camouflage principles was later in being r
nized than those which have to do with general conformi
background, or resemblance to specific objects in this.
colours or patterns which make the organisms inconspicuo
unrecognizable must be considered, regardless of backgr
For the recognition of these principles, chief credit must be
to the American artist, Abbott H. Thayer (*q.v.*), whose d
eries in this field were first announced in 1896, but wer
given wide publicity until 1909 (G. H. Thayer, *Concealing*
oration in the Animal Kingdom.) The first of these princip
that of counter-shading or obliterative shading, which had,
ever, been clearly stated by E. B. Poulton a few years e
This is a generalization of the fact that in the great major
animals, both terrestrial and aquatic, the dorsal surface o
body is more heavily pigmented than the ventral, while ther
gradient of decreasing pigmentation from one to the other. T
called attention to the fact, which he illustrated by solid m
that such a distribution of pigment makes for minimum visi
when the animal is lighted, as it most commonly is, from
head. Another principle, stressed by Thayer, which has
widely adopted in the camouflage both of animals and of
is that of ruptive and secant patterns. In such cases the n
continuity of the body's outline has been broken up by intr

ck or white or other pigment at the margins, or a less con-
ous general colour scheme of the body has been nullified
e observer by conspicuous markings which are quite ir-
nt to this. The effect is to render an object so treated
ognizable, even though it remains in full view. Under the
coincident disruptive colouring, H. B. Cott discussed a class
ses in which disruptive patterns were carried continuously
gh regions of the body which are not morphologically con-
us, *e.g.*, pigmented bars which run crosswise upon the hind
f a frog, but are evident only when the animal's legs are
y folded in the resting position. Similar pigmented stripes,
sed longitudinally, frequently include the eye. They divide
ody into two or more longitudinal sections and tend to
r it unrecognizable as a single organism of familiar form.

aptive Colour Change.—Many animals, belonging to sev-
f the major subdivisions of the animal kingdom, are able
nform their shades (as lighter or darker) or in some cases
actual colours, to those of the backgrounds on which they
n to lie. These changes are mediated through the eyes and
ntral nervous system, in some cases involving the endocrine
s. The effector organs are special cells in the skin or else-
, known as chromatophores. The most familiar of these
lack, white, yellow and red. Colour changes of this type
been most fully investigated in fishes, amphibia and reptiles
g the vertebrates, and in crustacea and the cephalopod mol-
among the invertebrates. The literature in this field has
e very extensive.

our changes resulting from chromatophore action are of two
sorts: (1) rapidly ensuing changes, often induced within a
inutes, or even seconds. These are brought about by the
gation or dispersion of pigment granules within the chro-
hores. The aggregated condition results in a withdrawal of
of the pigment from view, and thus to a paling of the
l. On the other hand, the dispersion of pigment leads to a
ing of the chromatophores, and thus of the surface of the
as a whole. These processes are frequently, but incorrectly,
ed to as contraction and expansion of the chromatophores,
as the outlines of the chromatophores are commonly little
ed.

e second type of color change (2) usually involves an in-
or decrease in the number of chromatophores present, as
s in the actual amount of pigment contained in the indi-
chromatophores. Such changes result from more prolonged
ction of the animal to the same stimuli which call forth the
familiar, immediate responses. In either case, it is important
e that the shade assumed, or the amount of pigment pro-
, is dependent not upon the absolute degree of illumina-
o which the animal is subjected, but upon the albedo of the
ound, *i.e.*, to the ratio of reflected to incident light. For one
of fish (*Girella nigricans*) it was determined that the amount
lanin present at the end of four months was about twice as
n specimens kept on black as in those which had been kept on
while the amount of the white pigment, guanine, was four
as great in the latter as in the former. The differences in ap-
ce, moreover, were much greater than these figures would
o indicate. The black-adapted specimens were nearly dead
the white-adapted ones were very pale gray.

lence that this capacity for pigmentary adjustment to back-
may be of lifesaving value to fishes has been obtained experi-
ly. Large numbers of fishes which differed widely in the extent
ich this adjustment had been carried were subjected to the
of fish-eating birds and of larger fishes. It was found that the
f less-adapted to more-adapted fishes among the casualties was
ently high, averaging about two to one. Aside from such tests,
er, the mere existence of the mechanism for adjustable colora-
ould seem to constitute strong evidence for the effectiveness of
ive coloration. For this complicated mechanism has been evolved
ndently in several unrelated branches of the animal kingdom.
rmore, so far as aquatic animals are concerned, no plausible
n except concealment has ever been suggested. To clinch this
ent more completely, it may be pointed out that the adjustment
e fishes to their backgrounds includes pronounced and appro-
changes in the disposition of light and dark areas on the skin
the pattern), which can have no significance except as affect-
pearance. The old familiar objection to the protective coloration theory that many of the presumed predators are not known to possess colour vision loses its force completely in the face of these facts. It is possible, however, that in some terrestrial animals, *e.g.*, lizards, the colour changes are secondarily concerned with the absorption or reflection of heat rays from the sun. This may be an important matter in desert species.

Warning (Aposematic) Coloration.—Many animals, especially among insects, which are themselves edible and inoffensive, have developed a superficial resemblance to other species, often widely unrelated to themselves, which are avoided by predators, owing to the possession of repellent or dangerous characteristics (*see* MIMICRY). This earliest discovered (Batesian) type of mimicry is believed to be supplemented by another (Müllerian) type, in which a number of species of animals that are equally obnoxious appear to have adopted a common, conspicuous livery, supposed to be recognized by predators as belonging to animals which had better be left alone. Thus, we have the warning colours of wasps and many other insects which are protected by stings, offensive scent glands, etc., of certain frogs which are known to be poisonous, and indeed of a wide variety of animals belonging to various groups. Experiments by a number of naturalists provide reasons for believing that birds, monkeys and perhaps some other animals do exercise choice in the selection of insects and tend to reject those having certain brightly coloured patterns. The results of such experiments are not wholly consistent, however, and the efficacy of warning coloration is perhaps more limited than has been claimed.

Recognition Colours.—This term has been applied to certain cases in which conspicuous markings are displayed, that may serve to identify an animal in the eyes of another of the same species, either at the time of mating or when they are flocking together for mutual protection. The white flag of the retreating cottontail rabbit, and the showy rumps of some of the deer are examples which are frequently cited in this last connection. According to A. R. Wallace, however, a large proportion of the differences of colour pattern which distinguish one species of birds or of insects from another are to be interpreted as recognition marks.

COLOUR AND SEX

In many species of animals the sexes differ more or less widely in colour. The most familiar examples of this are to be found among the birds, fishes and insects, although instances may be cited from some other of the major groups of animals. In cases where one sex is more highly coloured or more ornate than the other, it is usually the male which is so characterized. Much study has been devoted to the relation between sex hormones and the colours and other secondary sexual characters of animals, particularly of birds. In this group, as a rule, the castrated male retains the plumage colours of the normal animal, sometimes even to an exaggerated degree. The spayed female, on the other hand, takes on the colours of the male, and this may happen, without operation, as a result of disease of the ovary. These facts make it evident that the colours of the male in such species may develop in the absence of any hormone from the testis, while the colours of the normal female require the presence of a hormone from the ovary. The part played by the latter is further illustrated by the production of feminized males by grafting ovarian tissues into castrated cocks (capons).

In some birds and fishes these sexual differences of colour become greatly emphasized during the breeding season, diminishing or disappearing during the periods of sexual inactivity.

> In the Spring a fuller crimson comes upon the robin's breast;
> In the Spring the wanton lapwing gets himself another crest.

Among birds, these changes in plumage are usually due to the replacement of feathers, following the spring moult, less frequently to the shedding of the deciduous tips of feathers. In some cases, both among birds and mammals, it has been shown that the onset of moulting may be hastened or delayed through artificial control of the diurnal period of illumination. Shortening of this in the summer may lead to an earlier assumption of the winter plumage (or pelage), while the spring moult may be hastened by lengthening the period of daylight in the winter. In general, these alternations of plumage are not dependent upon the presence of sex hormones, and may follow their normal course in castrated birds. The same cannot be said, however, of the seasonal colour changes of some other parts, such as the bill and certain areas of skin, which are more likely to be under hormonal control. So far as known, the brilliant colours which are displayed in the spring by the males of many species of fresh-water fishes are hormonally controlled. They fail to appear in castrated males, while these same colours may be induced in females through the injection of the male hormone. In the latter case, actual quantitative increases of pigment may result, which persist for some time after the hormone treatment has been discontinued. In general, the nature and extent of the hormonal control of secondary sexual characters varies greatly from one organism to another. In insects such control seems to be lacking, sexual differences being more directly controlled by the hereditary complex, without the intermediation of hormones.

A question quite different from that of the physiological basis of sexual colour differences is that of the utility of these colours, if any, to the organism. Are the gorgeous colours of male birds, for example, of advantage to the wearers of these colours? Darwin, as is well known, answered this question in the affirmative with his hypothesis of sexual selection. The showy characters of the male plumage, he contended, arose through the continued selection by the females of more ornate mates. Darwin was able to point to cases among birds in which competitive display by the males and selection by the females seemed to be incontrovertible facts. And the extraordinary perfection to which certain colour schemes have been carried (*e.g.*, in the secondary wing feathers of the male argus pheasant) speaks for a level of aesthetic appreciation which certainly would not have been expected in a bird. However, the range of phenomena which can reasonably be explained by this sexual selection theory is certainly much less extensive than Darwin supposed, and in those cases for which it is regarded as relevant, the theory has undergone considerable changes in its formulation (*see* SELECTION and COURTSHIP OF ANIMALS). One alternative explanation which was offered by A. R. Wallace to account for certain sexual differences of coloration in birds would seem to have considerable inherent probability. Wallace contended that part of this difference might be due to the modification of the brooding female in the direction of concealment, the male being in less need of such protection. Indeed, the suggestion has been made by others that it might be advantageous to the species for the male to be more
spicuous during the nesting season in order to divert the attenti
predators from the (at that time) biologically more important fe

All in all, it must be admitted for a considerable proportio
sexual differences in coloration that no explanation can be found
indeed, that perhaps no explanation of a bionomic nature is
for. Knowledge of the animal's metabolism, when this is attained
perhaps be sufficient. And it might be added, that the same concl
is probably justified in regard to much of the coloration of anim
general. One does not inquire how minerals such as cinnib
malachite benefit from their respective hues and the question m
equally irrelevant in the case of many animals.

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Contribution No. 339

lours of Fishes.—If a beauty contest among animals were
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orange through yellows and greens to blue, with such mix-
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ore colours are combined to form definite markings, particu-
on the back. The lower surfaces are very often light gray,
or silvery. Black spots, bars or streaks are very frequent
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red.

e almost limitless range of colours and patterns that fishes
it is attributable to variations in the number, distribution
node of combination of only a few kinds of minute pigment
(chromatophores). Black pigment cells (melanophores),
containing myriad microscopic granules of melanin, are of
st universal occurrence. They produce black markings as well
neral shading and are involved in the elaboration of the iri-
nt greens and blues that appear on most fishes. These latter
sical colours" result from the play of light on tiny, needle-
crystals of guanine that overlie a background of melanin.
underlying black absorbs the red and yellow components of
When the iridocytes or leucophores (the guanine-containing
occur alone, a silvery or white appearance results. When
w pigment is added to an appropriate mixture of melano-
es and iridocytes, green is produced. Although certain fishes,
cularly in the families Belonidae and Cottidae, have a green
ical pigment in the bones, the greens and blues that appear in
kin are almost invariably the result of such combinations of
r cells as are mentioned above, rather than to special pig-
s or to special chromatophores. Yellow, orange and red areas
viewed under high magnification are stippled with yellow
ophores or red erythrophores, or with both of these caroti-
pigment cells. Pink, purple and lavender colours in fishes are
esult of different combinations and arrangements of erythro-
es and iridocytes, or to a mixture in fine pattern of spots and
ks of red and white, or of red and blue, or of red, blue and
. When small areas of yellow are interspersed the result is
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ISHES: COLOURS OF FISHES

by Carl L. Hubbs

olours of Fishes.—If a beauty contest among animals were ed, representatives of fishes would rank among contestants highest honours. The most colourful insects, the most resplend- birds of the tropics are rivalled in gorgeous colour by some es. It would be difficult to find, or paint, or imagine a more liant blue than that of the "neon tetra" of the home aquarists, ore intense red than that of the redbelly dace of American ams, a brighter silver than that of the ocean bream. These, of rse, are extreme (although not isolated) examples. Most es, like a large proportion of insects and birds, are coloured more brilliantly than are their usual surroundings.

he colours of fishes are most commonly greenish, olive or wn, but range through most of the visible spectrum from red orange through yellows and greens to blue, with such mix- s as orange-brown and purple common. The colours are ally mixed with black to produce dark shades and are often bined with white to yield such colours as pink and lavender. ngle colour may cover the entire fish but more commonly two nore colours are combined to form definite markings, particu- y on the back. The lower surfaces are very often light gray, te or silvery. Black spots, bars or streaks are very frequent nents in colour patterns, As in most groups of animals the erent species, and often the two sexes, are distinctively ured.

he almost limitless range of colours and patterns that fishes ibit is attributable to variations in the number, distribution mode of combination of only a few kinds of minute pigment s (chromatophores). Black pigment cells (melanophores), n containing myriad microscopic granules of melanin, are of ost universal occurrence. They produce black markings as well general shading and are involved in the elaboration of the iri- cent greens and blues that appear on most fishes. These latter ysical colours" result from the play of light on tiny, needle- crystals of guanine that overlie a background of melanin. e underlying black absorbs the red and yellow components of t. When the iridocytes or leucophores (the guanine-containing s) occur alone, a silvery or white appearance results. When ow pigment is added to an appropriate mixture of melano- res and iridocytes, green is produced. Although certain fishes, ticularly in the families Belonidae and Cottidae, have a green mical pigment in the bones, the greens and blues that appear in skin are almost invariably the result of such combinations of our cells as are mentioned above, rather than to special pig- nts or to special chromatophores. Yellow, orange and red areas en viewed under high magnification are stippled with yellow thophores or red erythrophores, or with both of these caroti- d pigment cells. Pink, purple and lavender colours in fishes are result of different combinations and arrangements of erythro- res and iridocytes, or to a mixture in fine pattern of spots and eaks of red and white, or of red and blue, or of red, blue and te. When small areas of yellow are interspersed the result is rown or some other secondary colour.

hese colour cells "expand" or "contract" in response to visual nuli, to the physiological state of the fish and to various inter- secretions and drugs. By this mechanism fishes are able to nge their appearance rapidly as they move from one environ- nt to another. What actually happens is that the pigment nules within the colour cells either become dispersed through- the whole star-shaped cell, to intensify the colour concerned; become aggregated into a dot at the centre of the cell, to omplish a fading of this colour.

he melanophores react particularly fast and those in different ts of the body may respond in the opposite way. As a result, nges in shade and in dark and light patterns may be accom- shed almost instantaneously. Changes in other colours, as from en to brown, are less rapid and less universal, and often re- re time for the decrease or elimination of certain pigments and for the increased manufacture or deposit of other biochromes. Actual changes in the amount of melanin and of guanine also take place when fishes are shifted from a light background to a dark one or *vice versa.*

Because of their capacity to change colour, fishes are past masters at camouflage. In this self-protective scheme the flat-fishes (flounders and soles) are famously adept. As these fishes move about over the sea bottom, the upper side (bearing both eyes) quickly takes on the colour of the surrounding mud, sand or rock. The pattern is also matched. Thus white fragments of shells are imitated by white spots on the body. Even the size and the abundance of dark and light objects are reproduced. These changes take place within a few minutes and are effected through the sense of sight. Similar transformations, even more rapid although not quite so perfect, are exhibited by other fishes, such as the groupers of tropical shore waters. Some reef fishes show vertical bars when at rest, but horizontal stripes when swimming.

Even more astonishing colour adaptations are attained by some fishes that live in marine plants of different colours, although the change may require days or weeks since some pigments in the skin must be lost and others gained. Thus the kelp blenny (*Heterostichus rostratus*) of California is wonderfully well concealed, whether it lives among the large brown "leaves" of the giant kelp (*Macrocystis*) or in the beds of eelgrass (*Zostera*). In the kelp it is uniformly brown, just like the alga. In the eelgrass it is striped with the intense green of this plant and with brilliant silver that matches the streaks of light between the slender blades of the plant. The two colour phases could hardly be more unlike and certainly appear to represent different species. They may, however, be changed back and forth experimentally.

In its imitation of the backgrounds the kelp blenny does not rely solely on perfect colour matching. It seldom swims horizontally. Ordinarily it heads up or down in line with the plants and may even waft its tail back and forth to simulate the movements of the leaves. A South American leaf-mimicking fish (*Monocirrhus*) drifts along just like a leaf. Baby gars (*Lepisosteus*) look like tiny twigs and float stiffly at the surface. Other fishes increase the efficacy of camouflage by imitating in posture or movement the environmental objects which they match in colour. In the light of such facts it is difficult to understand why some scientists doubt the reality of protective coloration and of adaptation in general.

Species that live on sand or other drab-coloured backgrounds do not possess a capacity to change colour that is at all comparable to the abilities of the kelp blenny. Those that live in a single kind of plant may imitate that plant only. The sargassum fish (*Histrio histrio*) does not show great range in colour variation but does simulate closely the floating sargassum weed in which it invariably occurs. The resemblance is so perfect that the fish is almost invisible even at close range as it slowly crawls about in the plant. Like other animals of the floating sargassum it shows white marks that look like the white growths of bryozoans on the alga.

Some biologists suggested that fishes and other animals take on the colour of the particular plant in which they live merely because they imbibe the plant pigment either directly by feeding on the plant or indirectly by eating smaller herbivorous animals. For fishes this is not true. Their colours are usually otherwise constituted and the changes can be effected when the experimental fish that are being kept in aquaria with differently coloured plants are fed the same type of food and are denied access to the plants by being kept in glass jars submerged in the aquaria. The last-mentioned test shows that the colour matching, like bottom mimicry by flatfishes, is effected somehow through the sense of sight.

That protective coloration involving only darkness and lightness in fishes really has survival value was experimentally proved (*see* COLOURS OF ANIMALS). Even before such proof was ob-

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tained field naturalists firmly believed that background mimicry arose through the evolutionary process of natural selection. The simulation of the background colour by fishes is too universal to admit of any other explanation. Nearly all species that swim near the surface—such as herrings, flying fishes and mackerels—are bright green or blue above, and are more commonly green inshore and blue offshore, just as is the ocean. The blue fishes of the coral reefs are the ones that swim into open water. Seen from beneath, all surface swimmers (*e.g.* halfbeaks and silversides) are silvery below and thus match the surface film which shines from below like a mirror. Most gobies, flatfishes and other species that live on the bare bottom are uniformly coloured or speckled or mottled with neutral colours. Tide-pool sculpins and blennies that habitually live among varicoloured aquatic plants, in contrast, are brightly and variously coloured, commonly grading from bright green through browns to red and often matching the peculiar pinkish-lavender of the coralline algae. Most fishes of the "twilight zone" of moderate depths are red, but in their own environment they are probably plainly coloured and concealed. Since red rays penetrate less deeply than the green, only green is reflected and it is absorbed. On a similar basis, coral-reef fishes that are red are almost invariably nocturnal. As is well known, red becomes invisible in dim light.

Cryptic (concealing) coloration is effected in almost all fishes, as in most other animals that live in light, by "obliterative countershading" (first stressed by the artists A. H. and G. H. Thayer). The back is enough darker than the lower parts to offset the shadows below, so that the whole image appears flat and indistinct. The exceptions among fishes interestingly prove the rule. Many deep-sea fishes, living below the zone of light, are as dark or darker below than above. The remoras (Echeneidae) are lighter above, but they adhere to sharks by their backs which are thus in the shadow. The "batensoda" (*Synodontis*), a catfish of the Nile, also reverses the usual scheme of countershading, but this fish habitually swims upside down. Some critics suggested that the darkening of the most exposed parts is the direct effect of light, but it was demonstrated that countershading is inherited and, therefore, that it is almost certainly the result of natural selection.

Although they render a fish in hand or in an ordinary picture very conspicuous, black bands and stripes are also regarded as concealing and protective, for at a moderate distance they disrupt the telltale fish outline. To be most effective such ruptive markings must extend to the very edge of the body and fins—and this they usually do. The eye is a particularly revealing organ, but in many fishes it is more or less completely obliterated by a black streak or bar or by radial markings. These markings pass across the whole eye or through the otherwise conspicuous pupil. That they are of definite significance is suggested not only by their frequent occurrence but also by the fact that they extend across several entirely different tissues. Streaks that pass through the pupil can commonly be resolved into seven parts: two outside the orbit; a pair on the sclerotic coat and conjunctiva; two on the iris; and one on the pupil. The sclerotic sectors extend under the orbital margins, so that the streaks remain continuous when the eye rolls. As Hugh B. Cott and William H. Longley pointed out, such "coincident disruptive" markings can hardly be the result of chance, or have any other basis than natural selection.

Usually the sexes in fishes are coloured alike, or the male in the spawning season is merely more intensely or more deeply pigmented, but in many species having a complicated breeding behaviour the male is much more colourful than the female. The guppy (*Lebistes reticulatus*) of aquarium fame is a familiar example. The "darters"—dwarfed perches that inhabit the riffles of streams in the eastern U.S.—exhibit nuptial male colours that are among the brightest in the whole animal series. Among marine fishes the dragonets show a similar sexual dichromatism. Darwin's theory of sexual selection (*see* SELECTION: *Sexual Selection*), though discredited of late, does seem to explain in part the de
opment of such sexual differences in colour. Sex recognition
intimidation of rivals, however, are probably more significant.

Some pigmentation appears to have a simpler significance
that it serves a physiological function primarily. Thus the mela
that is usually concentrated over the brain presumably shi
this vital organ from harmful effects of light rays. The bl
pigment in the peritoneal lining of the body cavity may simila
protect the viscera. The particularly black peritoneum of he
vorous fishes may furnish necessary protection for enzymes
aid in digestion of plant tissues. Melanin and guanine are
cretory products of metabolism. Their discharge through the
may serve the animal in this physiological way. But the pigm
also provide protective coloration. Evolution often "kills
birds with one stone."

Some critical biologists thought that the skin pigments
fishes merely represent excretions, or serve no function at
On this basis Jacob Reighard attempted to explain the extr
dinarily varied and brilliant colours of coral-reef fishes. He arg
that the fishes are adequately protected by their proximity to
retreats among the coral growths and are, therefore, immun
attack. The riot of colour (with hundreds of distinctive and
stant patterns) then "just happened." This "immunity the
of tropical fish coloration is not generally accepted, altho
other explanations are not wholly convincing. Alternative the
are (1) that the reefs are so brightly coloured as to render
fish inconspicuous; (2) that the bright markings are mostl
the ruptive category that destroy the fish's outline; (3) the col
may not appear as bright to some predators as they do to us;
(4) that the colours are recognition marks that keep the sch
intact and bring mates together and, since the species about
reefs are so numerous, the distinctive markings must be gre
varied. There is probably some truth in each theory.

There is little evidence that fishes with poisonous flesh
foul taste are conspicuously coloured for their own protect
as many insects are supposed to be. Even the dangerous
rays and the poison-spined madtoms (small catfishes of eas
North America) are as concealingly coloured as their innoc
relatives. "Warning coloration," however, may be exhibited
some of the surgeon fishes (Hepatidae), which have a nee
like spine on the tail. The flashy orange of the garibaldi or o
goldfish (*Hypsypops rubicundus*) of southern California app
to advertise the presence of this fish, which boldly fights to de
its home territory. Since revealing coloration seems seldom
have been evolved by fishes, it is not surprising that in this g
(unlike the Insecta) there are few examples of the mimicry
poisonous or unsavoury species by an innocuous one living
it. One probable case is that of an eel that simulates a poiso
sea snake.

Vivid colours were developed in some fishes by selec
breeding. From time before history the Chinese and Japa
produced goldfish breeds as bright and varied in colour as they
bizarre in form. In recent years aquarists bred a jet-black "
lie" (*Mollienisia latipinna*), a red "swordtail" (*Xiphoph*
hellerii) and many beautiful colour phases of the "platy" (*P*
poecilus maculatus). A tank of such fishes is a gorgeous h
ornament. (*See* also COLOURS OF ANIMALS.)

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(C. L. H

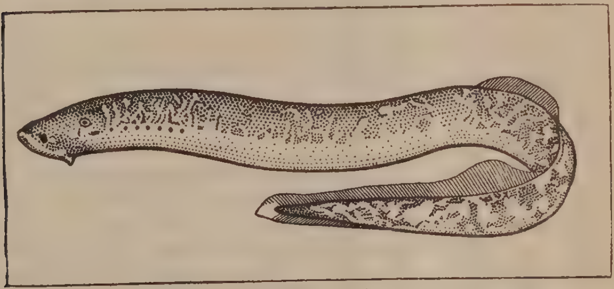
Contribution No. 340

CYCLOSTOMATA or MARSIPOBRANCHII

by Carl L. Hubbs

CYCLOSTOMATA or **MARSIPOBRANCHII,** a group of vertebrate animals, generally regarded as a class, comprising the lampreys (fig. 1) and the borers (*q.v.*). There are two types of borers, the hagfishes (fig. 2) and the slime-eels or *Myxine* (*q.v.*).

These are all aquatic creatures, smooth, slimy, scaleless and shaped like eels. The known species—about 50—inhabit the waters of the temperate zones. Most are marine, but a few lampreys are confined to lakes and streams and the sea lampreys spawn in fresh waters. The maximum size ranges from less than 6 in. to about 3 ft.



FROM JORDAN, "FISHES" (D. APPLETON-CENTURY CO.)

FIG. 1.—SEA LAMPREY, AN INHABITANT OF ATLANTIC COAST WATERS OF EUROPE AND NORTH AMERICA. IT ENTERS RIVERS TO BREED

Importance.—Most of the cyclostomes are regarded as harmful to man because they destroy food and game fishes. The larger lampreys attach themselves to fishes and drain their blood. In the Great Lakes considerable damage is thus done by the sea lamprey (fig. 1), which entered these waters by way of a canal and soon became very abundant, feeding extensively on lake trout and spawning in the lake tributaries. Efforts are made to control the increase of these lampreys by destroying the mature adults which are caught in a weir placed in the spawning stream. Marine food fishes are bled by seagoing lampreys, but suffer greater damage from the attacks of the borers. Both the hagfishes and the slime-eels eat their way into and through the flesh of food fishes. Large numbers of valuable fish are thus destroyed. Fish that are caught in nets or on set-lines are particularly subject to such loss. On the other hand lampreys are esteemed as food in many places and their larvae are extensively used as bait by fresh-water anglers. Adult brook lampreys, which are harmless because they do not feed, furnish, along with the larvae of all lampreys, considerable natural food for trout and other game fishes.

Scientifically the cyclostomes are of great significance, because they are the most primitive of the living vertebrates. The

(Continued)

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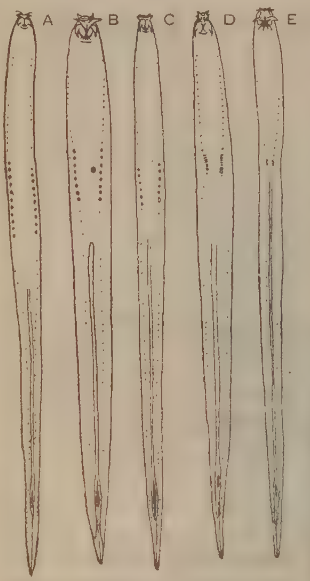
lamprey larva or ammocoete (fig. 4) in particular is regarded as providing the closest facsimile of the ancestor of the backboned animals. For this reason the ammocoete is recommended as one of the types to be studied in comparative anatomy courses. Adult lampreys and the borers depart from the ancestral form because they are specialized for parasitic existence.

Distinctive Characters.—The cyclostomes (or marsipobranchs) differ from all other living vertebrates in many important respects. None of their gill-arches have been converted into jaws, for which reason they are classified among the jawless vertebrates or Agnatha (a group which contrasts with the jaw-bearing vertebrates or Gnathostomata). The cyclostomes are also devoid of any trace of the paired fins (pectorals and pelvics), which, except for occasional loss through degeneration, are present in all other fishes and, in the form of limbs, are represented in all higher vertebrates. The muscular, protrusible tongue in all cyclostome fishes, and in the adult lampreys the buccal disc or funnel (figs. 3 and 5) as well, bear teeth which are composed of thin horny tissue rather than dentine or enamel. Instead of forming partitions between slits, the gills lie in spherical pouches which connect with the pharynx and with the exterior through tubes. The internal ear has only one or two semicircular canals, not three as in typical vertebrates (the horizontal canal is missing). The brain is small, primitive and distinctive, and the brain case is incomplete, especially in the borers. The skeleton is wholly cartilaginous, without any trace of calcification. The notochord is persistent throughout life and is nowhere constricted. No vertebrae proper (centra) are formed. The olfactory organ is a single median sac with an internal opening into the cavity of the pituitary and an external opening that lies on the midline either on the top or at the front of the head. On the basis of the narial structure some authorities classify the cyclostomes, along with certain extinct groups discussed below as the Monorhini. All other vertebrates are said to be diplorhine, for they have paired nostrils, with one sac on each side of the head.



FROM DEAN, JOUR. COLL. SCI. UNIV. TOKYO

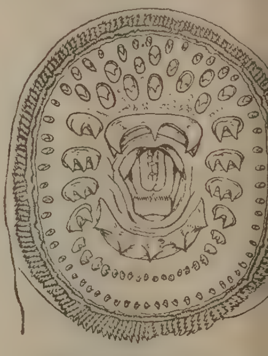
FIG. 2.—FOUR HAGFISHES AND A SLIME-EEL

A. *Polistotrema stouti*, California; B-C. Japanese species of *Eptatretus*; D. *Paramyxine*, from Japan; E. *Myxine garmani*, Japan

Classification.—The Cyclostomata are divided into two subgroups, which are very different in anatomy, appearance and habits:

	Hyperoartii (lampreys)[1]	*Hyperotreti* (borers)
Nasal opening	On top of head	At front of head
Pituitary canal	Closed internally	Opening into pharynx
Cartilaginous rings around this canal	Lacking	Developed
Pineal eyes	Easily visible	Degenerate
Eyes	Well developed	Vestigial
Oral funnel	Developed	Not present
Teeth	On disc also	Only on tongue
Tentacles about mouth and nostril	Lacking	Six, supported by cartilage
Number of gills	Always seven	5 to 14
Gill-openings	Close to head	Remote from head
Internal gill tubes	United	Separate
Duct on left side, pharynx to exterior	Lacking	Developed
Branchial skeleton	A conspicuous basket-work	Greatly reduced
Dorsal fin	One or two well developed	None or only a tr
Neural arches	Present	Lacking
Dorsal and ventral roots of spinal nerves	Distinct	United
Kidneys	Compact organ	Separate
Eggs	Minute, without horny shell	Very large, with horny shell
Development	With larva and metamorphosis	Direct (young muc like adult)
Spawning place	Gravel in streams	Ocean floor
Feeding on	Fish blood	Fish flesh
Type of parasitism	External	Internal

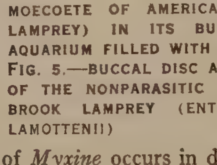
The differences between the lampreys and the borers are extensive and so fundamental as to lead some authorities think that the two groups are unrelated. They appear, however, to have had a common ancestor.

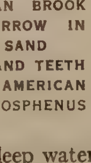


BY COURTESY OF CARL L. HUBBS

FIG. 3.—BUCCAL DISC AND TE OF A PARASITIC LAMPREY, ENT PHENUS TRIDENTATUS (PACIFIC LAMPREY)

The Hyperoartii or lampreys may be classified into three families. The chief family, Petromyzonidae, comprises all the northern hemisphere species. The well-known sea lamprey, *Petromyzon marinus* (fig. 1), occurs on both sides of the Atlantic. Three related genera, *Eudontomyzon, Entosphenus* (figs. 3-5) and *Lampetra,* occur in Eurasia as well as in North America. The primitive genus *Ichthyomyzon,* with more species than any other, inhabits only the fresh-waters of eastern North America. *Caspiomyzon* is confined to the Caspian sea basin. About half species of Petromyzonidae are of the dwarfed nonparasitic br type, with weak teeth (fig. 5). Nearly all of these have ari through degeneration from different parasitic kinds, and he they are named as distinct species (in the genera *Ichthyomy* *Eudontomyzon, Entosphenus* and *Lampetra*). The distinc lampreys of the southern hemisphere are placed in two famil Geotriidae and Mordaciidae, each with a single genus (*Geo* and *Mordacia*). These southern genera live along the coasts Chile, New Zealand and Australia. Like all lampreys they spa in fresh water.





FROM JORDAN, "FISHES" (D. APPLETON-CENTURY CO.)

FIG. 4.—LARVAL LAMPREY (AMMOECOETE OF AMERICAN BROOK LAMPREY) IN ITS BURROW IN AQUARIUM FILLED WITH SAND

FIG. 5.—BUCCAL DISC AND TEETH OF THE NONPARASITIC AMERICAN BROOK LAMPREY (ENTOSPHENUS LAMOTTENII)

The Hyperotreti or borers c prise the Eptatretidae, or fishes, with the genera *Epta tus, Polistotrema* and *Para xine,* and the Myxinidae or sli eels, with the one genus *My* (fig. 2). That genus is cha terized by the single external opening on each side. It is proached by *Paramyxine,* w has the gill-openings closely proximated (fig. 2). For reason some authors prefe unite the Eptatretidae with Myxinidae. All members of groups are marine. One spe of *Myxine* occurs in deep water off Panamá but all other kn Hyperotreti are inhabitants of temperate waters—in wes North America, Japan, New Zealand, Chile, Patagonia and S Africa. Fewer than 24 species are recognized.

Life History.—All lampreys spawn in the spring on gr beds in streams. The marine species migrate into the stream breed, passing over dams and other obstructions by inching way up the vertical walls, to which they adhere by their suc disc. The males arrive first on the spawning grounds and o prepare the nest. By adhering to and tugging out pebbles ession is formed. The female then maintains a hold on a while the male clamps onto the female and twists around the eggs are extruded and fertilized. Then by further tug- ne pebbles above the depression are loosened, so that they rried down to surround and cover the eggs. By the time awning act is completed the adults are emaciated. They recover, but invariably die.

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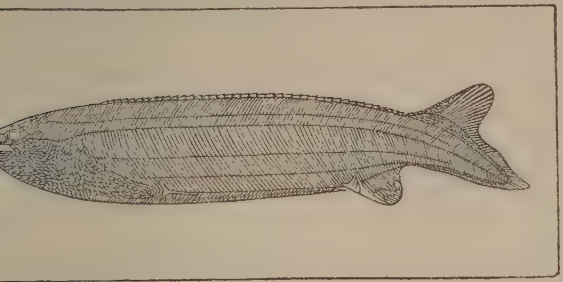
[1] The characters are those of adult lampreys. In several respects the lamprey larvae agree with the Hyperotreti.

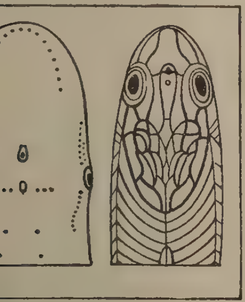


"THE DOWNTONIAN FAUNA OF NORWAY"

6.—PHARYNGOLEPIS OBLONGUS, AN ANASPID FROM THE UPPER- IAN OF NORWAY. THERE WAS A SERIES OF SMALL GILL-OPENINGS ID THE HEAD, AS IN THE LAMPREYS

er about two weeks the eggs hatch and the larval or am- te life, that lasts several years, begins. The several size , each resulting from one year's spawning, prove this point. ormlike, toothless, nearly blind larvae (fig. 4) live in bur- n the bottom of mixed sand and mud, coming out at night d on the organic ooze which is strained through the thick the hoodlike mouth.

er at least three years of such life the ammocoete rapidly orms in late summer and fall into the adult form. The eye es much larger and better developed, the hood is replaced disc and the cirri by teeth, the nostril opening moves from ont to the top of the head, and many other changes take simultaneously. The body becomes rounder in cross-section, sh firmer and the colour brighter. During this transforma- metamorphosis the lamprey shrinks considerably in length. n after metamorphosis the sea lampreys become silvery and eyed in preparation for life in the ocean, to which they tly migrate. Some of the nonparasitic brook lampreys pass h this same stage, known as the macrophthalmia, as though in racial remembrance of the former seaward journey, though this trip has been abandoned for millenia.



AER, VIDENSK. SKRIFT, OSLO

.—A COMPARISON OF THE SEEN ABOVE, OF THE LIV- AMPREY (PETROMYZON) AND ILURIAN FOSSIL ANASPIDA CHOLEPIS), SHOWING ESSEN- IMILARITY

All parasitic lampreys feed and grow rapidly on their nutritious diet of fish blood. Those that remain in fresh water live thus for a year. A larger size is reached in the sea but it is not known how long the marine forms live as adults, for they are seldom encountered. After their growth has been attained and the sex products ripened the parasitic species spawn once and then die, to complete the life cycle.

The nonparasitic species metamorphose at a size at least as s do their parasitic relatives, but the teeth are poorly devel- and the gut shrinks to a solid strand. Without taking any hey complete, over-winter, the ripening of the sex products had begun before the metamorphosis. Like the parasitic s they then spawn and die.

hagfishes and slime-eels (fig. 2) deposit a large, yolk-filled This is enclosed in a protective horny shell and is attached bottom of the sea by threadlike tendrils. The development wer than in lampreys and the young are much larger when hatched. They look much like the adults, into which they gradually develop without a metamorphosis. Thus in life history as well as in structure the Hyperotreti are very unlike the Hyperoartii.

Evolutionary History.—The fossil record as well as the evidence from comparative anatomy indicates that the Cyclostomata are cousins of the earliest and lowest vertebrates. The oldest fossilized remains of vertebrate animals, found in the Silurian deposits with traces in the yet more ancient Ordovician rocks, prove on close study to be similar in many respects to lampreys and borers. Superficially the fossils (figs. 6-12) bear little resemblance to their modern relatives, which, in correlation with their parasitic habits, are highly specialized in some respects and in other ways much degenerated. In fundamental anatomy, however, they were much alike. Thus the extinct forms resembled the cyclostomes in lacking jaws, for the anterior gill arches remain unaltered. They appear also to have lacked true paired fins, though in some species flipperlike flaps were developed in place of pectoral fins. The extinct forms agreed further with the cyclostomes in gill structure and in having had only two semicircular canals in the internal ear. Some of the extinct groups had, like the cyclostomes, a single median nostril.

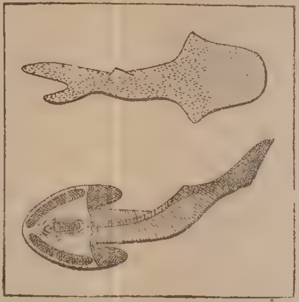
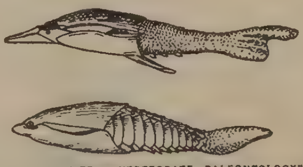


FIG. 8. AFTER TRAQUAIR, LANKESTER "TREATISE ON ZOOLOGY" (A. & C. BLACK, LTD ; FIG. 9. AFTER WOODWARD "PROCEEDINGS," BY COURTESY OF GEOLOGISTS' ASSOCIATION

FIGS. 8 AND 9.—FOSSIL AGNATHA

Above: *Thelodus scoticus*, one of the Coelolepida from the Silurian of Lanarkshire. Below: *Cephalaspis murchisoni*, from the Devonian of Herefordshire. It was covered with bony plates

Most of these early fishes, and naturally those that are best known because most thoroughly preserved, were heavily armoured with dermal bone—hence the group name Ostracodermi that has often been applied to them as a whole. On these grounds many paleontologists have regarded the bizarre armoured fishes as the direct ancestors of the more ordinary modern types. It is more logical to assume, however, that both the armoured and the progressive types were derived from unarmoured fishes with the usual fish form. The highly specialized mailed kinds were probably evolved to provide protection from such enemies as the gigantic "water scorpions" of early times. Furthermore such types had a much greater chance than their slender, soft-bodied and probably free-swimming ancestors to be fossilized and well preserved in the rocks. The more highly evolved, heavily armoured types persisted throughout late Silurian time and all of the Devonian, along with the earlier jawed or gnathostome fishes which are classified as the Placodermi. None of the Ostracodermi are known to have survived beyond the end of the Devonian, but some primitive member of the Agnatha must have persisted, to give rise to the living group with which we are dealing. In conformity with an evolutionary rule the highly specialized group died out, while some generalized relative lived on.



FROM ROMER, "VERTEBRATE PALEONTOLOGY" (UNIV. CHICAGO PRESS)

FIGS. 10-11.—FOSSIL PTERASPIDA OR HETEROSTRACI

Above: Poraspis, from Silurian of Spitzbergen
Below: Anglaspis, from Devonian of England

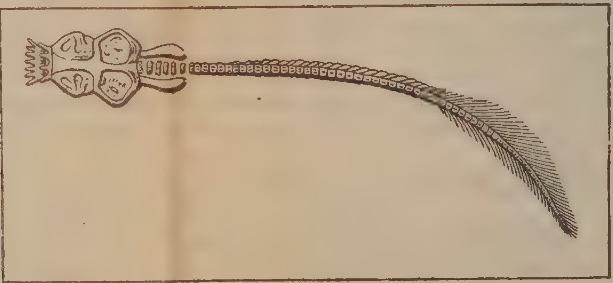
Fossil Relatives.—Since the cyclostomes are the only living Agnatha or jawless vertebrates their relatives are to be sought exclusively among the extinct fishes. Five groups, commonly treated as orders, all Paleozoic and none persisting beyond the Devonian, show evidence of relationship with the lampreys and borers.

(1) In some ways the most lampreylike of the fossils were the Anaspida (fig. 6). These Silurian and Devonian creatures seem primitive because of their small size (none exceeding 10 in.), their almost ordinary fish form and their small scales, which apparently

overlaid the muscle segments. These characters and more particularly the rather straight contour of the back, the terminal rather than inferior mouth and the hypocercal or reversed heterocercal tail (with the body axis extended into the long lower caudal lobe), indicate that they escaped their enemies by swimming at the surface of the water. As in the cyclostomes, they had the eyes lateral and a single nostril in front of the third or pineal eye (fig. 7); and the gill-openings formed a row of pores on each side.

(2) The Cephalaspida (or Osteostraci) also had a median, superior nostril and a row of porelike gill-openings, but differed from the Anaspida (and from the cyclostomes) in having the head enclosed in a flat bony shield (fig. 9). The tail was heterocercal (with the body axis extending into the long upper lobe of the caudal fin) and the eyes were set close together on the top of the head. All these characters indicate that these armoured fishes lived on the bottom. They varied in length from a few inches to about 2 ft.

(3) The Coelolepida (fig. 8) were small to medium-sized and were completely covered with minute scales (denticles) that did not overlap. Structurally these fishes are poorly known, but from superficial resemblances they are thought to have been related to the Pteraspida. Indeed they may have belonged to that group and by some authorities they have been so classified. Or they may have been ancestral to the Pteraspida. Denticles thought to have belonged to one of the Coelolepida are known from the Ordovician.



BY COURTESY OF THE TRUSTEES OF THE BRITISH MUSEUM

FIG. 12.—PALAEOSPONDYLUS GUNNI, TWICE NATURAL SIZE, FROM THE SILURIAN OF SCOTLAND

(4) The Pteraspida (or Heterostraci) were armoured fishes (figs. 10-11) that closely resembled the Cephalaspida. Both groups were abundant in late Silurian and early Devonian times and disappeared completely by the end of the Devonian. Some of the very earliest known vertebrates, fragments of dermal plates from the Ordovician rocks, are thought to have been pteraspidans, because of the microscopic structure. In this group the armour lacks the bone cells that were characteristic of the Cephalaspida. The paired eyes were far apart and there was no dorsal nostril. The olfactory organs, which were close together but paired, are supposed to have opened into the mouth cavity. Like the anaspids the typical pteraspidans had a straightish dorsal contour, a reversed heterocercal tail and little depressed bodies—all indicative of surface-swimming habits. None exceeded 1 ft. in length.

(5) The Devonian group known as Cycliae or Palaeospondyloidea is recognized for one of the most problematical of the fossil vertebrates, Palaeospondylus (fig. 12), which by some has been thought to be an ancient lamprey or lampreylike animal. If so, the living lampreys must be very degenerate, for they lack the vertebral centa that are well developed in the fossil. Other zoologists regarded it as a larval arthrodire. The remains of this 1 to 2 in. fishlet abound in one quarry in Scotland and have been very thoroughly studied. Nevertheless, its relationships remain uncertain. Opinions differ as to whether or not it had gills or paired fins.

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Contribution No. 341

DIAN OCEAN

by H. U. Sverdrup
and R. H. Fleming

IAN OCEAN, the name applied to the region bounded
north by India and Iran (Persia); on the west by Arabia
rica; on the east by the Malay Peninsula, the Sunda Is-
Australia and Tasmania; and on the south by Antarctica.
trary separation from the Atlantic is made at the longitude
Cape of Good Hope (20° E.) and from the Pacific at the
de of Tasmania (147° E.).

ocean is more than 10,000 km. (6,200 mi.) wide between
thern points of Africa and Australia and narrows steadily
the north, where it is separated by India and Ceylon into
lf of Arabia and the Bay of Bengal. Two adjoining seas
t with the Gulf of Arabia, the Red sea through the Strait
el Mandeb and the Persian gulf through the Strait of
Because of the concentration of maritime traffic in low
es, the Indian ocean is often considered to be a tropical
out actually it extends to latitude 70° S. and the Red sea
rsian gulf reach to 30° N.

Indian ocean has an area of 74,917,000 sq.km. (28,929,000
and is the smallest of the three oceans, comprising only
of the ocean-covered portion of the earth. The two ad-
seas included in these figures are relatively small, the
a covering 438,000 sq.km. (169,000 sq.mi.) and the Persian
9,000 sq.km. (92,300 sq.mi.).

Indian ocean receives few large rivers, the chief being the
zi, the Shatt-al-Arab, the Indus, the Ganges, the Brahma-
nd the Irrawaddy. J. Murray estimated the total land area
g to the Indian ocean at 13,080,000 sq.km. (5,050,000
(1.3 the area of Europe), more than two-thirds that drain-
the Pacific. The Pacific, however, is more than twice as
s the Indian Ocean. In addition to the rivers mentioned,
thwestern and northwestern monsoons in the tropical re-
n the eastern side of the Indian ocean bring heavy rains,
ere is heavy rainfall also in the neighbourhood of the equa-
calms. Therefore, the surface water in these regions con-
ery little salt, particularly in the Bay of Bengal into which
e great rivers from the mainland.

ief of the Ocean Floor.—Large portions of the ocean bed
unexplored. In the latter part of the 19th century, H.M.S
enger" and the German "Gazelle" and "Valdivia" pro-
a general understanding of the topography which was later
led by the expeditions of the "Sealark" and many British
ships. The "Discovery II" made extensive cruises, begin-
1929, in high latitudes and in the western part of the
The oceanographic vessels "Willebrord Snellius" and
II" worked in the open ocean, and the "Ammiraglio Magna-
the Red sea. In 1933–34 the "Mabahiss" explored the
estern part of the ocean.

ngitudinal ridge, the Indian ridge, extends from India to
tica and separates the Western Indian and Eastern Indian
s. Although similar in general location to the Atlantic
it is much wider and does not extend so near the surface.
northwestern part of the ocean the ridge is divided with
evations extending toward the coast of Africa and separat-
e Arabian, Somali and Mascarenes basins. The longitudinal
is continuous at depths less than 4,000 m. (13,000 ft.).
gh the western part of the ocean is divided into a series of
the Eastern Indian trough extends from the Bay of Ben-
Antarctica. Between Tasmania and Antarctica is the Mac-
ridge, continuous at depths less than 4,000 m. (13,000 ft.)
separates the deep water from that in the Pacific. West
Kerguelen ridge, which forms the southern part of the
dinal ridge, there is deep-water connection with the At-
These features influence the deep-water circulation and
stribution of properties.

The greatest depths are found in the Sunda trench, a narrow depression paralleling the Sunda Islands, where soundings of 7,455 m. (24,460 ft.) have been obtained. Depths of about 6,500 m. (21,300 ft.) exist in the central part of the Eastern Indian trough (Wharton Deep, 19° S., 100° E.). The Red sea, with an average depth of about 500 m. (1,600 ft.) and maximum depth of 2,800 m. (9,200 ft.) is separated from the open ocean except for a narrow channel only 100 m. (330 ft.) deep. In contrast, the Persian gulf is a shallow sea with an average depth of only 25 m. (80 ft.). The mean depth and volume of the Indian ocean are described in OCEAN AND OCEANOGRAPHY.

Islands.—Madagascar, the largest of the ocean's islands, rises from a plateau about 1,500 m. (4,900 ft.) deep extending out from Africa. Ceylon and Sokotra are continental islands. The Laccadive, Maldive and Chagos Islands rise from the central part of the Indian ridge, while those extending from the Seychelles to Mauritius rise from the westward extension of the ridge and are separated by deep water from Madagascar. The Andaman and Nicobar Islands rise from a ridge extending southward from Cape Negrais. Between the ridge and the Malay peninsula there is a deep "gulf" opening only to the south. Many oceanic islands, such as Mauritius, Crozet and St. Paul's, are volcanic. Those in tropical seas are often coral formations or possess coral reefs.

Bottom Deposits.—The characteristics of sea-bottom sediments are described in OCEAN AND OCEANOGRAPHY because they are common to all oceans. The greater part of the Indian ocean north of 50° S. is covered with Globigerina ooze. At depths greater than 5,000 m. (16,000 ft.) the calcium carbonate content is small and the deep basins, especially the Eastern trough, are covered with red clay. Radiolarian ooze is found in some of the deeper basins, and Diatom ooze covers a broad band in higher southern latitudes. Eighty-six percent of the main basin (excluding adjacent seas) is covered with pelagic sediments, Globigerina ooze covering 47%, red clay 22%, Diatom ooze 17% and Radiolarian ooze 0.4%. The remaining 14% of the bottom and the adjacent seas are covered with terrigenous sediments or shallow-water calcareous deposits (coral sands and muds). Glauconite is abundant in sediments off the African coast and calcareous sediments predominate in the Persian gulf and on many of the coasts and oceanic islands in tropical latitudes.

Compared with the Atlantic and the Pacific oceans, the high proportion of pelagic siliceous oozes is quite striking, but this is the result of the shape of the ocean and the relatively large extent of the Diatom ooze band in the south.

Meteorology.—In no oceanic division does the regular half-yearly alternation of all the factors in weather conditions and particularly the winds play such an important part as in the monsoon regions from 10° S. northward of the Indian ocean. From Oct.–Nov. to March–April northeast winds prevail in the north latitude and northwest winds in the south latitude; from May–June to Sept.–Oct. south and west winds prevail. In the Arabian sea between Sokotra and the Maldives these southwest monsoons are very violent and are dangerous even to modern steamship traffic. From the earliest times the voyages of the native sailing vessels between India and Africa have been regulated by these alternating winds. The southwest monsoon brings rain to the whole of India; the northeast monsoon is predominantly dry. Southward from the latitude of the Seychelles—Chagos—Cocos islands, the southeast trade wind prevails throughout the year, and south of 30° S. the west winds which are generally particularly strong between 40° and 55° lat., and of which in the 19th century the fast sailing ships bound for Australia and China took advantage. The tropical storms, especially of

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Mauritius, are much dreaded; they follow a parabolic course from east to west then southward and back to the southeast, and occur in the summer season. In the Arabian sea and the Bay of Bengal these hurricanes are, fortunately, rare and occur only once or twice a year, in April–May and Oct.–Nov., that is to say, at the periods when the monsoons change. In the Hooghly Delta off Calcutta the high waves which accompany the storms are dangerous and have caused the loss of thousands of lives.

Surface Currents.—Over the northern part of the Indian Ocean the surface currents change with the monsoon. During the northeast monsoon the currents flow toward the southwest and west, crossing the equator, and between the easterly current maintained by the monsoon and the westerly current maintained by the southeasterly trade wind a strong counter current flows east in about 10° S. The southwest monsoon appears as a continuation of the southeast trade wind of the southern hemisphere which in crossing the equator turns from a southeasterly to a southwesterly direction. In the season of the southwest monsoon westerly currents prevail to somewhat north of the equator and turn then around toward the north. A strong northerly flow is found particularly off the Somali coast and the southeast coast of Arabia, where upwelling lowers the temperature near shore.

In the southern part of the Indian ocean a counter-clockwise circulation prevails with westerly currents to the north of 20° S. and easterly currents maintained by the prevailing winds to the south of 40° S. These easterly currents represent part of the large Antarctic circumpolar flow. The south equatorial current divides when reaching the coast of Madagascar, sending one branch north and another branch to the south. The northern branch turns around the northern end of Madagascar and flows south through the Mozambique channel and continues as the Agulhas current to Cape Good Hope. Only a small fraction of the waters of the Agulhas current continues into the Atlantic ocean, and by far the greater body of water mixes with the waters of the circumpolar current and is carried to the east with that current. In the region of mixing the surface temperature shows a great variability with alternating streaks of cold and warm water.

Deep-Water Circulation and Character of Deep Water.—No large amount of deep water is formed in the Indian ocean by sinking of surface water, but the deep basins are filled by water which enters the Indian ocean to the south of Africa and is therefore similar to the deep water of the South Atlantic.

The deep-water circulation appears to be very slow compared with that of the Atlantic. Along the bottom the coldest water advances to the north and at a depth of about 1,000 m. (3,300 ft.) Antarctic intermediate water of low salinity also flows north and can be traced nearly to the equator. Between these two northerly flows deep water returns to the south and rises toward the surface near the Antarctic continent. To the north of the equator the movement of the deep water is probably extremely slow.

Conditions are somewhat complicated by the outflow of high salinity water from the Red sea along the bottom of the Strait of Bab el Mandeb. This Red sea water sinks, mixes with the surrounding water and spreads at depths of 1,000 to 1,500 m. (3,300 ft. to 4,900 ft.). To the north of the equator it can traced as far as Ceylon, and to the south of the equator to ab 25° S. off the coast of Africa. The Red sea water corresponds the Mediterranean water in the Atlantic ocean, but since the o flow from the Red sea is relatively small it exercises a less wi spread influence upon the salinity distribution at moderate dept

Below a depth of about 2,000 m. (6,600 ft.) the temperat of the deep water decreases from about 3° C. (37° F.) to ab 1.5° C. (35° F.) at the bottom and the salinity remains nea constant at 34.8 ‰ (per mille).

Temperature.—North of the southern tropics the temperat of the surface waters is at all times higher than 20° C. (68° and in the equatorial latitudes over 25° C. (77° F.); in the ea ern half it is generally above 27.5° C. (81.5° F.); in the sea and the Persian gulf the temperature often rises to ab 30° C. (86° F.). South of 40° S. the water quickly cools that off Kerguelen (49° S.), even in summer the temperature been found to be no more than 2° C.–3° C. (36° F.–37° The isotherms run mainly from west to east, and their cours not diverted by currents to so great a degree as in the Atlanti

Salinity.—The saltiest surface water is found (a) in Arabian sea and (b) along a belt extending from south Australia to south Africa, the highest salinity in this belt oc ring at the Australian end. In both regions the salinity exc 36‰ (per mille). In the monsoon region west of Sumatra throughout the Bay of Bengal, owing to rainfall and the inflo rivers, the salinity is diminished to 34‰ and at the mouth the Hooghly channel to as little as 30‰. In the northern tions of the Red sea and the Persian gulf, on the other hand, salinity is sometimes as high as 40‰. South of New Amste and Saint Paul the salinity, as also the temperature, qui diminishes, and south of Kerguelen as far as the Antarctic there is a uniform Antarctic water of salinity 33.7‰.

Ice.—In the extreme southern part of the Indian ocean ice and icebergs from the Antarctic are encountered in all sons. In October the northern limit of the pack ice lies in a latitude 58° S. and in March it closely follows the coast of Antarctic continent in about lat. 65° S. The average nort limit of icebergs lies in about 45° S.

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Contribution No. 342

IARINE BIOLOGY

by Martin W. Johnson

IARINE BIOLOGY is concerned with all kinds of living
gs that exist in the sea, or that are by nature dependent upon
sea at its surface or at its coastal boundaries. It deals not
with the kinds of marine organisms but also with their life
ories and interrelationships. It endeavors to learn and explain
vays in which the various physical and chemical factors (tem-
ture, light, pressure, currents, salinity, plant nutrients, etc.)
ie environment operate, together with the organic factors en-
g the organisms to survive and to populate every niche of the
n from the Arctic to the Antarctic and from the surface to
sal depths. Insofar as investigations have been made, no part
is great environment is without some type of animal life.

nds of Organisms Found in the Sea.—The plant life of
sea consists only of the Thallophyta (the most primitive
o of plants) and a few angiosperms or flowering plants. No
es or ferns occur in the sea. The larger of the marine plants
he green, brown and red algae and the eelgrasses. The algae
nchored to the substratum, mainly in depths less than 50
y means of "holdfasts." There are no true roots or vascular
ms, hence the plants absorb their food from the water bath-
heir general surfaces. Typically they reproduce by means of
oscopic spores which develop into inconspicuous male or
le plants called the gametophyte generation. This generation
rn gives rise to the spore-forming sporophyte generation.
eelgrasses have an underground stem and true roots, which
n nourishment from the mud and sand in which they grow.
are found in depths ranging up to 15 m. The submerged
rs are pollinated by floating pollen, after which true seeds are
ed.

e attached plants form an important source of food for ani-
in the shallow water. However, the chief producers of
ary food in the sea as a whole are the microscopic plank-
diatoms and holophytic dinoflagellates. These tiny plants
xceedingly numerous. Under favourable conditions they re-
ice at a prodigious rate by means of simple cell division;
being independent of the bottom, they are capable of growing
here in the sea where light and nutrient supply are favour-
More will be said about their importance later.

cteria are abundant and widely distributed in the sea. They
gnificant mainly in the decay of organic material. There are
marine moulds, but they are of little importance in the
my of the sea.

e animal kingdom has its greatest development in the sea.
f the major divisions (phyla) are to be found there and
(Ctenophora, Echinodermata, Phoronidea, Brachiopoda,
ognatha) are strictly confined to this habitat. About 44%
e recognized classes, the second highest division, are exclu-
marine while only about 6% are exclusively nonmarine.
Amphibia are the only type of vertebrates not represented in
ea. The fishes are primarily marine. The reptiles are repre-
d by true snakes and turtles. Many birds are marine in their
ndence upon the sea for food. Some, for example the alba-
s, spend much of their life far from land, which they fre-
only for nesting. The principal marine mammals are the
s, porpoises, sea cows, seals, sea lions and sea otters.

the invertebrates, the crustaceans, molluscs and worms are
kably diverse and abundant. In the sea, the Crustacea occu-
position comparable numerically to that held by the insects
nd. Strangely enough, the insects are almost completely ab-
rom the sea. Only one is known to live its whole life there.
others skip on the surface or live in the debris on the fore-

life histories of marine animals are extremely diverse.
ver, it can be stated that most of the invertebrates undergo
type of indirect development in which there is a free-swimming stage (*see* INVERTEBRATE EMBRYOLOGY). Usually the eggs of these animals are spawned free in the water where they are fertilized. Commonly they possess only a small amount of yolk to feed the developing organisms. Correlated with this, they develop first into self-sustaining larvae totally unlike the parents. These larvae drift about in the water for a period of several days or even weeks. Finally, a complete metamorphosis takes place in which the structure and habits of the parent animals are assumed. Animals with this type of life history produce an exceedingly large number of eggs. This serves to compensate for the heavy losses attending a free larval existence. Alternation of generations is another striking feature of many marine animals, especially of the coelenterates. For example, the common jellyfish (hydromedusa) represents the solitary sexual generation, which alternates with the colonial asexual generation. The latter is a sessile hydroid that superficially resembles a tiny plant. Direct development (in which the organism assumes the adult form by gradual growth) is characteristic of the fishes, cephalopods and certain Crustacea.

The Categories of Life in the Sea.—It is possible to classify the marine organisms into three large groups, *i.e.*, the benthos, nekton and plankton, on the basis of their general habitat and locomotory effectiveness. The benthic animals and plants are those that live upon the sea floor either attached, burrowing or creeping. It includes such animals as barnacles, snails, crabs, worms, etc. All of the larger algae and some diatoms, etc., are benthic. In the nekton are placed all of the animals such as fishes, whales, seals, squids, etc., that are capable of swimming effectively against water currents and in making migratory journeys. In the plankton (*q.v.*) are grouped all of the animals and plants, usually microscopic in size, that float in the water with little or no effective swimming and therefore drift about with the water currents. The plankton is divided into (1) phytoplankton, which includes the diatoms, holophytic dinoflagellates and a few other types, and (2) zooplankton, which includes representatives, either adults or young, of nearly all animal groups from the protozoans to the fishes. The floating eggs and larvae of the benthos and nekton are known as the temporary or meroplankton in contrast to the permanent or holoplankton which comprises the organisms that are planktonic during their entire lives.

Zones of Life in the Sea.—As an aid to study of marine biology the environment is commonly classified into a number of divisions and zones based mainly upon a combination of physical and biological criteria (*see* fig.). The two main divisions are the benthic and the pelagic. The former comprises all of the bottom and the latter all of the water overlying the bottom. They are sharply defined, and typically the subdivisions of each are also clearly recognizable, but there is often a good deal of overlapping at the borders (*see* DISTRIBUTION OF ANIMALS). The upper part of the benthic division is known as the littoral system. It is subdivided into an upper or *eulittoral zone*, extending from shore to a depth of about 50 m., and a *sublittoral zone*, from 50 m. to a depth of about 200 m. (considered the edge of the continental shelf). The deep-sea benthic system consists of an archibenthic zone, from 200 m. to about 1,000 m., and an abyssal-benthic zone, from there downward to the greatest depths. Within the littoral zone there is an "intertidal zone" comprising that part of the foreshore that is alternately covered and exposed by the tides. This zone may be broad or narrow, depending upon geographical and topographical position. In the intertidal zone the attached plants are usually low growing and flexible to withstand the wash of waves. The kinds of animals occurring in this area depend mainly upon the type of bottom, whether rocky or sandy, etc., and upon the degree of exposure to action of the sea. The

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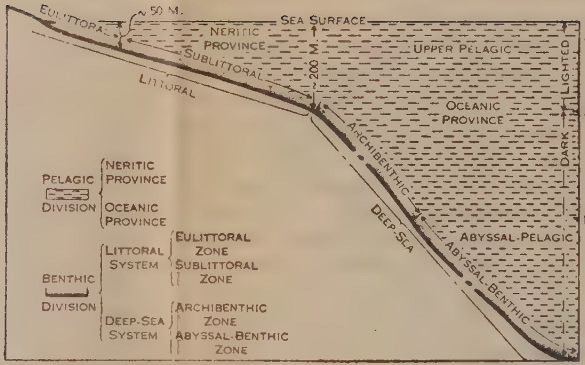

FROM SVERDRUP, JOHNSON AND FLEMING, "THE OCEANS" (PRENTICE-HALL, INC.)

THE MAIN DIVISIONS OF THE MARINE ENVIRONMENT

abundance of life developed in any given section of the zone is determined largely by the degree to which the bottom material can be shifted about by the waves or by other factors such as dilution by rain or runoff, exposure to heat or freezing, or abrasion by ice. During periods of low tide, many animals, such as clams and worms living in mud or sand, find protection from desiccation or heat in their moist burrows. In general, the intertidal animals of rocky exposed coasts are relatively hardy. Often they are provided with heavy streamlined shells and suckerlike structures to hold the close-fitting shell firmly against the rock. Thus they gain protection from impact of waves, and are enabled to retain some water during low-tide periods. Many molluscs, tube worms, and barnacles are firmly and permanently cemented to the rock. The shore crabs and other crustaceans are conveniently flattened to enable concealment in narrow crevices and under rocks. Weak, fragile forms such as the erect lacy bryozoans, sea fans, sea pens, spider crabs, etc., are rare in this zone since they require either the constant mechanical support of water or are unable to tolerate violent water movements. Competition for living space is a serious factor to many littoral animals. It is often critical to the survival of post-larval stages seeking space for attachment.

In the deeper part of the littoral zone the attached plants are more abundant and characteristically larger than in the intertidal area. In the kelp beds of the Pacific the long-stalked *Nereocystis* and *Macrocystis* may grow to a length of more than 100 ft., though most algae are much shorter than this. It is in the subdued light of this zone that we find the beautiful red algae, some of which are used in the manufacture of agar (*q.v.*).

In the sublittoral zone some solar light is available but it is much reduced, hence few plants of importance are found there. Coralline algae grow in the shallower portion where the bottom is rocky or covered with coral or shells. Benthic animals may be abundant in this zone, for much food is washed out in the form of detritus from the upper littoral zone and the production of planktonic plants in the overlying water is favoured by the physical and chemical conditions. (*See* OCEAN AND OCEANOGRAPHY.)

In the deep-sea benthic system (which includes more than 90% of the bottom of all oceans combined) solar light is still detectable in the shallower (archibenthic) zone while in the abyssal zone perpetual darkness prevails except for the faint and weird light produced by some of the animals living there. The waters are uniformly cold, being but a little above the freezing point for vast areas of the ocean floor. No primary food is produced within these zones. It must be precipitated from the lighted waters above or be carried in with water currents from the littoral zones. The scarcity of primary food results in a scarcity of animals in the abyssal depths. In general, chemical conditions are not favourable for production of planktonic plants in the lighted waters of the oceanic province which lies above the deep-sea zones. Much of the plant material that is produced is eaten or disintegrated in the course of sinking to the great depths where the abyssal mals live. The deep-sea animals, in general, are modified repr tatives of familiar shallower-water types. As in the lit fauna, many species are similar to or related to ancient types, indicating that they too have existed for a very long

The Pelagic Division is the home of the plankton and ne It comprises all of the water overlying the floor of the sea. coastal waters to depths of about 200 m. are the Neritic Prov and the waters with greater depths are the Oceanic Prov Though no sharp line can be drawn between these two, yet has its characteristic planktonic plants and animals. For exa the temporary plankton, *i.e.*, the eggs and young of bottom mals and the jellyfish with sessile stages, is a conspicuous pa the neritic plankton. Neritic diatoms frequently form re spores that sink to the bottom when temperature or other l conditions become unfavourable. In the oceanic province the greater stability of living conditions, and the formation of sp of the neritic type is not the rule. Resting spores that sink t bottom in great depths could have no value unless they b turned to the lighted surface, and this is unlikely. The su oceanic animals are often blue in colour. Many are hyaline the deep waters of the oceanic province where solar light is reduced or absent the colours are mostly red, brown, violet-b or black. Light-producing organs are notably conspicuous, cially among the fishes living at about 300–500 m. These or may be arranged in specific patterns, and the colour of the produced may also be specific. This is perhaps an aid to the mals in recognizing their kind, for eyes are functional in depths and are often unusually large or protruding, the bett intercept the faint rays of light. Below mid-depths blind f and squids are found, and the light-producing organs are red or absent. But the bottom-feeding fishes of great depths pos eyes, made useful presumably because of the luminescenc benthic animals.

FUNDAMENTAL ECOLOGICAL FACTORS IN THE S

I. PHYSICO-CHEMICAL

The biologically important physico-chemical factors are us interactive and affect the organisms in various and complic ways. It is useful, however, to discuss a few of these factors their general applications under separate headings.

The Sea-Water Medium.—Sea water is chemically a suitable biological medium, for it contains in solution all of elements necessary to the structure and maintenance of organis The ratios of the major salts entering into the salinity of water are similar to those of body fluids, and the total concen tion of the salts is also similar to that found in the bodie most marine organisms, particularly in the invertebrates. T there is maintained a favourable osmotic relationship between external environment and the internal body medium. This tonic relationship lessens the labour required by excretory or in maintaining the proper concentration of fluids within the and precludes the need of impervious membranes. This is in trast with the hypertonic condition of fresh-water forms w the body fluids are more concentrated than the water and th fore tend to become diluted through osmosis.

Sea water is normally alkaline and tends to remain so bec of its buffer capacity, which resists any change in pH (hydr ion concentration). This is a boon to the many calcium-pre tating forms.

The density of the water offers the mechanical support ne sary to unarmoured or flaccid forms such as jellyfishes and anemones, and provides the buoyancy required by all pe forms.

Hydrostatic pressure increases about one atmosphere for ten metres of depth. This restricts the vertical range of m animals that are intolerant to pressure change, but it does not to eliminate life from the abyssal depths, where the pressur upward of 1,000 atmospheres, *i.e.*, about 15,000 lb. per sq.in. pressure can be tolerated because it is equal inside and outside also the plankton and detrital food of the non-predaceous members of an association are brought into the area through the agency of water currents or precipitated from the water above. Where environmental conditions are rigorous with respect to physical and chemical factors, many potential members are eliminated but those suitable to survive may become very abundant, owing to absence of serious competition for space and food. Among individuals within the community there are always other more restricted and intimate relationships such as commensalism, symbiosis and parasitism.

MARINE BIOLOGICAL METHODS

The preliminary procedure in investigating the organisms in any area of the sea is descriptive and consists of identifying, describing and cataloguing the many species of animals and plants that occur within the area. This is a very large task, especially in hitherto unstudied areas. It requires the labour of several investigators, each of whom is a specialist in one or more of the biological groups involved. The reports and monographs published by these specialists give formal diagnosis of each species and record its distribution. These reports are tools in the hands of subsequent investigators dealing with analytical studies such as the ecology of the individual species or groups of species. (*See* ECOLOGY, ANIMAL.)

The methods of collecting and of analyzing and studying the material after it has been collected depend upon the objectives of the investigations, whether taxonomy, embryology, ecology, etc. These objectives also determine the number and kinds of physical or chemical observations that are made in the field in conjunction with the collecting. The equipment and procedures available for the study of the inorganic factors of the environment have been vastly improved since the famous "Challenger" Expedition of 1873–1876, which has been the model for subsequent work. Accurate reversing thermometers now enable determination of temperatures at any desired depth and the bathythermograph provides a continuous temperature record downward from the surface. Light intensity can now be accurately measured with photoelectric apparatus lowered into the sea. Chemical procedures assure proper evaluation of oxygen, salinity and the major plant nutrient salts. Coring devices are available for use in collecting undisturbed bottom sediments for study of microorganisms in the muds. Sonic depth finders provide numerous or continuous soundings. These are important devices, some of which have grown out of the needs of marine biologists for accurate and quickly obtained data to use in ecological interpretations. Others are borrowed directly from other branches of marine sciences—physics, chemistry and geology—and applied to biological research.

In ecological work the numbers of individuals of any species occurring in a unit space in a given area are determined and correlations made with the external environment. The numerical and nutritional relationships to other animals and plants in the community are also determined in order to ascertain the relative importance and interdependence of the various members. For embryological studies of the animals, living specimens are brought to the laboratory where the processes of fertilization, cleavage and larval development are observed under the microscope. Similarly, the algal spores shed from living plants are cultured under experimental conditions to learn their life histories. The planktonic diatoms are likewise grown to ascertain their nutritional requirements and rate of photosynthesis under various conditions of light. Numerous other studies; for example, the osmotic balance, oxygen consumption, reaction to light, etc., require living material for experimental procedures under controlled conditions. But the common objective of experimental and field observations is to understand the organisms in nature and under natural conditions. For these reasons marine biological laboratories are established at seasides where live material is available and natural conditions observable (*see* below).

Benthic collecting in the intertidal zone requires but simple equipment for digging out the burrowing forms or prying loose those that are attached to rocks or piles. When statistical studies are involved, the area covered and its relative position with respect to mean low tide is carefully recorded, for nowhere else in nature are specific organisms confined to such a narrow vertical range as are some of the species living within the intertidal zone.

In deep water a dredge operated from a power or sail boat is used. Where the bottom is smooth, various types of trawls are commonly used instead of the dredge. For quantitative surveys in shallow water, some type of "grab"—such as the Petersen grab—that scoops up the material from a known area of bottom (*e.g.*, $\frac{1}{4}$ sq.m.) is employed.

In collecting the microscopic plants that make up the phytoplankton, fine silk nets are used for qualitative work; but, for quantitative studies, "water bottles" (cylindrical metal containers of a litre or more capacity) that can be closed at any desired depth are used to obtain a definite volume of water together with its passive organisms.

In the analysis of phytoplankton collections, an aliquot sample of the water collected by means of the water bottle is centrifuged to concentrate the diatoms and dinoflagellates in the sample. The organisms thrown down in this manner are then counted on a ruled slide or in a counting chamber under the microscope. From these counts calculations are made giving the number of plants per litre of water. Sometimes the whole sample is filtered through a fine net and examined, and computations made as above.

Chemical methods are also used for determining the amount of phytoplankton. With this method extractions with acetone are made of the yellow-green pigments in the chlorophyll. The pigment obtained in this manner in a known volume of acetone is determined colorimetrically with an arbitrary standard of 25 mg. of potassium chromate and 430 mg. of nickel sulfate dissolved in one litre of water. The results are reported as "pigment units" which amount to 3.3×10^{-3} mg. of organic carbon. The ratios, by weight, of the major constituents of plankton are carbon, 41; nitrogen, 7.2; phosphorus, 1.

The zooplankton is more sparse and irregular in its distribution than is the phytoplankton, hence larger nets of coarser bolting cloth are used, or other filtering devices—such as the Hardy Plankton Recorder or the Clarke-Bumpus Plankton Sampler—that likewise strain a relatively large quantity of water are employed.

The volume of the material collected with the nets is determined by allowing it to settle in graduated cylinders or by draining off the fluid. The organisms of interest are counted and the stages of development noted. If the volume of water filtered in collecting the sample can be determined, the number of organisms or the volume in cubic centimetres is given for one cubic metre of water or for one square metre of ocean surface.

The methods for collecting nektonic animals for study of marine biology are essentially those of commercial fisheries; various trawls, nets, setlines, traps, etc., being the standard equipment. Much of the biological material studied or the statistics accumulated are obtained directly from the commercial catches of fish or whales. This is particularly true where the biological research is conducted by some government agency for the conservation of marine fisheries resources. Statistics are kept relative to the size of catch, size of fish or whales, area fished, gear and effort involved. In the study of migration of certain fishes like the salmon or the halibut, living specimens are tagged from commercial catches, liberated and later recovered largely from similar catches. Our information on the biology of whales has resulted largely from co-operation between scientists and whalers. (*See* ZOOLOGICAL COLLECTING: *Marine Collecting*, for other details.)

MARINE BIOLOGICAL STATIONS

Marine biological stations are laboratories (usually operated by universities or government agencies) where the various types of research and studies related to marine life can be most efficiently carried on. For this reason they are established at seasides where living plants and animals can be readily collected for laboratory study or observed under natural environmental conditions. They are usually situated well away from harbours that are likely to be

age or oil. Aquaria with circulating sea
r the purpose of display or study of live
pped for dredging or trawling are often
the laboratories, and row boats are avail-
ore. Some laboratories are also equipped
servations in shallow water. Many of the
officially open only during the summer
e attended by investigators and students
ther schools. Some of the stations now
engaged mainly in research.

rine biological station is at Naples. It was
Anton Dohrn. Another well-known Mediter-
ed by Prince Albert I at Monaco. The largest
Hole, Mass., where there are also an ocean-
isheries laboratory, combining to make this a
ne biological studies. Other important U.S.
t Island, Maine; Cold Spring Harbor, Long
Island, Md.; and on the Pacific coast at La
ove, Calif.; and Friday Harbor and Seattle,
search Board of Canada operates stations at
St. Andrews, N.B. Prior to World War II
ation, a large excellently equipped laboratory
dinavian countries operate several good sta-
The principal British station is that founded
l Association of the United Kingdom and is
Plymouth. Other English and Scottish bio-
ons are at Cullercoats in Northumberland;
Man; Millport and Aberdeen in Scotland and
15 or more French stations, the better known
ago de Banyuls. Russia has about 11 stations
fisheries research. In the Orient Japan has
tions, and before 1936 China maintained four
stations. There are fewer tropical and semitropical stations. Amon
the better known of these is the Bermuda station.

Throughout the world in 1937 there were about 105 marine bi
logical stations and 25 purely fisheries research stations. About on
half of the former included fisheries investigations and biological i
struction as part of their activities, otherwise the work was main
general biological research. A growing need for a wider scope in m
rine research has led to establishment of oceanographic laborator
where biological work is carried on as actively as before but wi
greater facilities to study all phases of the environment as a whol
particularly at sea. *See* T. W. Vaughan (1937) for detailed accoun
of the various institutions.

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sult also the reports identified with the various marine expeditio
especially the "*Challenger*," "*Albatross*," "*Siboga*," and "*Discovery*
among the most useful journals for marine biology are the *Jour*
of the Marine Biological Association of the United Kingdom; Jour
of Marine Research; Journal of the Fisheries Research Board of Ca
ada; and the various publications of the International Council for t
Exploration of the Sea; *Internationale Revue der Gesamten Hyd*
biologie und Hydrographie. (M. W. J.)

Contribution No. 343

OOLOGICAL COLLECTING:
ARINE COLLECTING

by Martin W. Johnson

MARINE COLLECTING

arine collecting presents a number of special problems be-
e of the vastness of the sea, the great depth at which many
ne animals live and the difficulty of caring properly for many
he delicate forms while in the field. The marine collecting
comprises about 71% of the earth's surface, and most parts
be reached only by sea-going vessels. About 77% of the
om area is covered by water over 9,800 ft. (nearly 2 mi.) in
h, and the greatest depth is over 6 mi. Animal life is found
only on the bottom but also to some extent throughout the
e water mass, hence collecting on the high seas must be
ted to all of these circumstances, and it is therefore an un-
aking for specially organized and equipped expeditions. How-
, a most important part of marine collecting can be done
simple equipment in the intertidal zone or in shallow
tal waters. Fortunately, also, it is here that the greatest
dance and variety of plant and animal life is produced. The
t depths are relatively barren.

arly systematic collecting of bottom (benthic) animals was
ted to the intertidal and shallow water zones and it was be-
d (E. Forbes, 1843) that no animals lived at depths greater
about 300 to 700 metres. Before this time some collections
been reported by Sir John Ross (1819) from depths of 1,800
res, but these were discredited as being uncertain. However,
860 undisputed collections of marine animals were made
a submarine cable which, in being repaired, was raised from
pth of 2,160 m. where the animals had attached and grown.
s, interest was stimulated in collecting and exploring the
t depths to determine what mysteries of life might lie hidden
his forbidding environment and to learn the factors control-
life in the sea. Likewise, the vast abundance and impor-
e of the planktonic or floating life was not realized until
t 1846 when J. Müller is said to have used for the first time
ne-meshed cloth net drawn through the water as a collecting
ce.

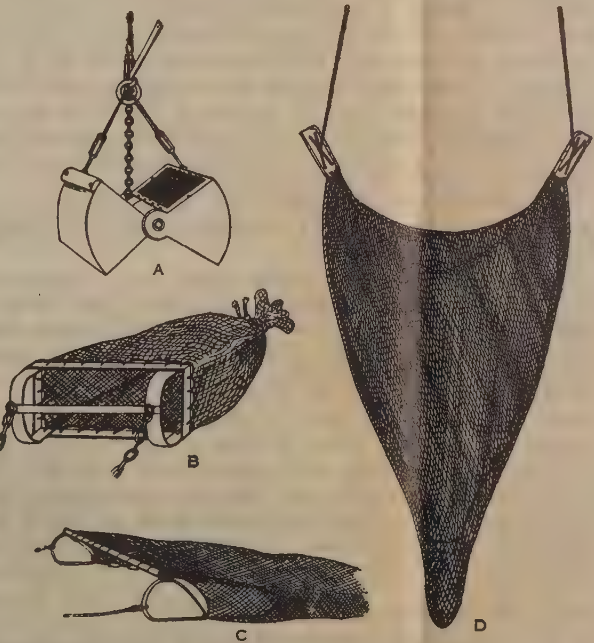
he earliest large-scale marine collecting expedition was that
I.M.S. "Challenger" 1873–76, during which time vast areas
he Atlantic and Pacific were explored. Since then much
ine collecting has been done by research ships of various
ons, and animal life has been collected and studied from
y positions in all oceans, but vast coastal and oceanic areas
still unexplored by collectors. In all of these expeditions the
cting has usually not been an end in itself but rather a nec-
ry part in gathering data of importance to fisheries or to gen-
marine biology (*q.v.*).

lethods and Gear Used in Collecting.—Collecting is
er for qualitative or quantitative purposes. The first is the
oler because the objective is merely to obtain the organisms,
reas in the second it is necessary to know as nearly as possible
many species or individuals were taken from a definite area of
bottom or from a known volume of water. This requires care-
collecting in order that the numbers can be correlated with
r ecological data bearing on the distribution and biology of
organisms.

ntertidal and shallow-water collecting for bottom-living ani-
s requires only simple equipment. Where the bottom is com-
ed of mud and sand, a long-handled shovel or rake is needed
digging out the burrowing forms and a screen for sieving out
smaller animals from the loose material. A mixture of mud
sand usually yields more animals than does a beach of pure
l. The latter, however, is not without its characteristic type
ife and sometimes in surprising numbers, especially certain
ms (*Thoracophalia*, for example), the little sand crabs (*Eme-*
, etc.), the wedge shells *Donax* and, at high-tide level, the sand hoppers. The animals that are found on mud-sand bottoms are numerous and varied. Commonly they are of the burrowing types, such as clams and worms, and their presence is revealed to the collector by little characteristic mounds, holes or markings on the surface of the mud. The best collecting for variety of forms is, however, on rocky or coral reefs. Here a strong chisel-edged bar is useful for prying loose limpets, mussels, sea stars and many other forms that are attached to the rocks, or for breaking up old coral and shell encrustations or for rolling over rocks to expose retreats that usually teem with life. The tide pools left by the receding tide yield many additional forms including nudibranchs, fishes and cephalopods. The attached algal plants should be searched for the many animals that attach to or hide among their fronds. Eel grass (*Zostera*) beds in shallow water are favorite collecting places. Here attached to or living among the leaves can be found an abundance of hydroids, bryozoa, skeleton shrimp and such characteristically eel-grass inhabitants as the sea anemone *Epiactis*, and the sessile jellyfish *Haliclystus*. Dip nets or hand seines drawn through the disturbed eel grass are sure to capture a variety of small fish and invertebrates.

Among the more profitable of collecting places are the submerged portions of wharf piles or floats where fouling organisms and the animals associated with them can be scraped off with rakes or dip nets. Here the wood too should be examined for the destructive wood-boring forms such as the shipworm *Teredo* and the gribble *Limnoria*.

Shallow-water benthic animals are often cast up on the beach by action of waves during storms, and sometimes also pelagic forms normally found only on the high seas are drifted ashore in this way. The collector takes advantage of this and also watches for the many small animals that he can find among the rootlike holdfasts of deep-growing seaweeds that have been torn loose from the bottom and drifted onto the beach.



FROM SVERDRUP, JOHNSON, AND FLEMING, "THE OCEANS" (PRENTICE-HALL)

FIG. 3.—GEAR FOR BIOLOGICAL COLLECTING: (A) PETERSEN GRAB. (B) DREDGE. (C) BEAM TRAWL. (D) OTTER TRAWL

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Deep-water collecting for benthic animals requires special equipment operated from boats provided with winches for reeling in line. The standard equipment includes dredges or trawls (fig. 3, B,C,D). The dredge consists of a strong iron frame to which a bag or net of strong web or wire screen such as hardware cloth is attached. This bag retains the animals that are scooped up from the bottom by the edge of the dredge frame as it is dragged forward over the bottom by a long wire cable or rope operated from a winch aboard a slowly moving ship. The edge of the frame may be constructed with flares or teeth to dig into the bottom. Usually the frame is rectangular and is about 2 to 5 ft. in length, depending upon the size of boat and winch facilities. The trawl, a modification of the dredge, is designed to fish free in the water or to skim over the bottom rather than to dig into it. There are three main types: the beam, the Agassiz and the otter trawls. In the beam trawl the mouth of the net is held open by a beam of iron or wood so arranged as to glide over the bottom on sledlike runners, while a lead line holds the lower lip of the net in contact with the bottom. The Agassiz trawl is a modification of the beam trawl. In it the mouth of the net has both upper and lower lead lines, hence it fishes properly no matter which side of the trawl is applied to the bottom. For scientific collecting a 10 or 15-ft. beam is ample but for commercial fishing the beam may be much longer. In the otter trawl the mouth of the net is held open by means of otter boards so arranged that they are forced apart by the water when being towed forward by a line attached to each.

The trawls are more efficient than are the dredges for collecting active animals such as fish or shrimps. They are not practicable for collecting on rocky bottoms. Dredging and trawling in very deep water is a laborious operation, sometimes requiring as much as 12 hours for one haul at a depth of 3000 fathoms. Often only a few animals are caught at these depths but these are of exceptional interest because of their strange habitat.

Dredges and trawls are most useful for qualitative collecting because it is difficult to know accurately how much bottom has been covered in sampling. For quantitative collecting of small sessile animals in shallow water the Petersen grab is used (fig. 3, A). It consists of hinged heavy iron jaws that are held open by a mechanism that is released when the instrument strikes the bottom. Upon being lifted from the bottom the jaws close over a definite area (usually 0.1 sq. metre) of the bottom, scooping up the bottom material together with the contained animals.

The collecting of pelagic animals may be considered in two parts: (1) the floating animals (zooplankton) and (2) the strong-swimming animals (nekton).

The zooplankton, composed mainly of such feeble swimmers as copepods, euphausiids, chaetognaths, various larvae, and the dinoflagellates, is collected in various ways all of which utilize some type of screening device, such as the plankton tow net. In simple form the tow net (fig. 4) consists of a ring to which is attached a conical bag of gauze, usually of silk bolting cloth which is so woven that the screening apertures are uniform and not readily changed in size. When the net is drawn through the water, the organisms are screened out and concentrated in a bottle or jar fastened into the apex of the net. There is a great range in size of plankton organisms, hence the fineness of the net used is determined by the minimum size of the animals to be caught. For general zooplankton collecting a No. 8 type bolting cloth with screening apertures of about 0.205 mm. is practicable, though many of the smallest organisms escape. Some protozoan forms, for example the smaller ciliates and dinoflagellates, pass through the finest nets. To obtain a quantitative estimate of these small members of the plankton, it is necessary to collect them by means of centrifuging a known quantity of sea water.

For collecting planktonic animals from subsurface levels, closing nets are used. These can be lowered to the desired depth a there opened by means of a special mechanism operated by "messenger" which glides down the towing wire. When the t is completed the net can again be similarly closed to prevent a further fishing while it is being hoisted to the surface.

Some quantitative nets are provided with a small cyclome which records the amount of water that has flowed through t net. George H. Clark and D. F. Bumpus (1940) developed plankton sampler of this type which can be used in series, th collecting plankton from several water strata simultaneous A. C. Hardy (1939) devised a continuous plankton recorder which collects quantitatively at a given depth (10 m.) along the route of a ship back of which the recorder may be towed for many miles.

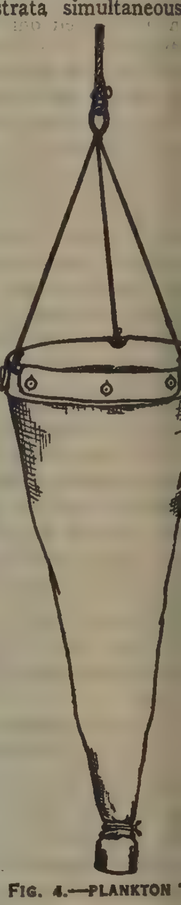

FIG. 4.—PLANKTON NET

For collecting fishes and other nektonic animals, nets, seines, hooks and harpoons are used, but these are best considered under fisheries (*q.v.*), nets and seining.

The use of lights for attracting and collecting swimming animals at night sometimes yields many forms not readily collected during the daytime. Even some bottom living forms may swim to the surface where they can be scooped up with hand nets.

Care of Material Collected.—A definite part of the task of collecting is the care of the material while in the field or en route to its destination in the laboratory, museum, or aquarium. Unless means are available for a steady or frequent change of fresh sea water in which to keep the animals, most of them soon die. Benthic animals when crowded into a bucket, as is often done, usually survive best if covered with wet seaweed rather than with water which soon becomes warm and exhausted of its oxygen or charged with metabolic wastes. If the animals are of a flabby type and need the support of water, a quantity of sea lettuce (*Ulva*) kept in the bucket with them is of aid. Intertidal and tidepool animals are the hardiest and should be collected for aquarium specimens in preference to the more delicate forms of deep water. On expeditions or on long collecting trips most or all of the material will need to be preserved in a manner consistent with its fu use for study or display. Alcohol, 70%, is the best general -servative, but formalin is more economical and serves as where some hardening of the tissues is not deleterious. Five p formalin to 95 parts sea water is suitable to preserve most s animals. Basic formalin may be used for organisms such as foraminifera and echinoderm larvae with delicate calcare skeletons if alcohol is not available.

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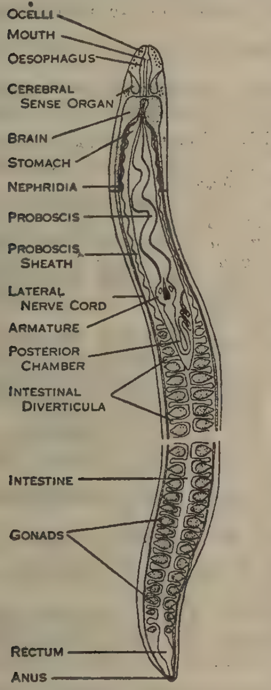
Contribution No. 344

EMERTEA

by Wesley R. Coe

EMERTEA (NEMERTINEA). The nemerteans, or nemer- s, commonly called ribbon worms, which constitute the in- ebrate phylum Nemertea, are characterized by the soft, ex- ible, ciliated body, without external indication of segmenta- and without distinct body cavity, the internal organs being rated by gelatinous parenchyma; the body is provided with ghly specialized eversible proboscis and a usually straight in- ine opening at the posterior end of the body (fig. 1). There no external appendages except the caudal cirrus, sucker and acles, found in a few species.

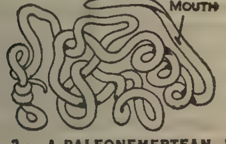
emerteans vary greatly in size and shape; some are long, flat- d and ribbonlike and may grow to a length of 1 to 4 metres 3); others are threadlike and from a few millimetres to ral metres in length when mature; some are cylindrical (fig. 2); others are broad and flat. In nearly all forms the body may be contracted to a small fraction of the length which it has in full extension.



. 1.—ORGAN SYSTEMS OF A LONEMERTEAN

Most of the species are marine and littoral; many of them burrow in sand or mud; others hide beneath stones or creep about among algae and other growths between tide marks or in shallow water. The members of the tribe Pelagica are strictly bathypelagic, with flattened, gelatinous bodies adapted for floating idly or swimming sluggishly far beneath the surface of the deep oceans. A few species inhabit fresh-water streams and lakes; others have migrated to the land, living in moist earth or beneath fallen logs, stones or dead foliage. Certain species live as commensals in the mantle cavities of pelecypods or of tunicates, in the canals of sponges or beneath actinians; and finally there are several species which are parasitic on the gills and among the egg masses of crabs.

The nemerteans are all carniv- s, feeding on protozoa, turbellarians and other worms, molluscs, taceans and the young of all the invertebrates with which they e in contact. Some have such distensible mouths that they can ur animals of almost their own diameter. Others have small ths and suck in only the juices of their prey.



. 2.—A PALEONEMERTEAN, PRO- HALOTHRIX SPIRALIS

When food is not obtainable the nemertean is able to live for a long time upon the nourishment to be obtained from its own tissues. Individuals of some species may thus survive starvation for a year or more. In the meantime the body may have shrunk to a small fraction ($\frac{1}{20}$ or less) of its former size. Some of the small forms may ive unfavourable conditions by coiling their bodies in a firm cyst ecreted mucus, to resume activity at a later time.

lany of the species are brightly coloured in life, with shades of red, ge, yellow, green, gray and brown predominating. Some have a orm coloration, while others have definite patterns or markings ontrasting colours, with rings, longitudinal lines, spots or reticula- s. The physical basis of the colour patterns consists of pigment ules secreted within the epithelial cells of the integument or in underlying connective tissue cells or both.

lorphology and Physiology.—The morphological characteristics of a nemertean are shown in fig. 1. Although there is no external indication of segmentation, most of the internal organs are arranged metamerically. The body is covered with a layer of ciliated epithelial cells, interspersed with mucous and sensory cells. The epithelium is supported on a basement layer of firm gelatinous tissue, beneath which, in the Heteronemertea, is a thick layer of mucous glands and connective tissue, the cutis. The musculature of the body wall consists of two or more layers of circular, spiral and longitudinal muscles which enable the worm to carry on rapid changes in body form. Locomotion is accomplished by creeping or gliding, by alternate elongation and contraction, by twisting spirally or, in a few species, by swimming. The proboscis is sometimes used as an aid in creeping or burrowing.

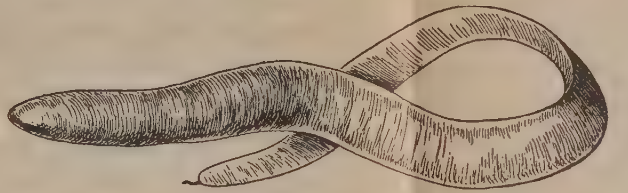


FIG. 3.—A HETERONEMERTEAN, CEREBRATULUS MELANOPS

The *proboscis* is formed by an invagination of the anterior body wall and consequently has essentially the same muscular and epithelial layers but in reverse order. In its normal position within the body it lies within the proboscis sheath, which forms a closed, saclike cavity, the rhynchocoel, filled with a corpusculated fluid. In a few species of hoplonemerteans the sheath is provided with paired diverticula. The anterior end of the proboscis is anchored firmly into the tissues of the head near the brain, while the posterior end commonly terminates in a long retractor muscle attached to the proboscis sheath or in some species to the musculature of the body wall in addition. The proboscis is everted through the rhynchodeum by the combined action of its own muscles and such contractions of the musculatures both of the sheath and body walls as will exert pressure on the fluid in the rhynchocoel. It is withdrawn by reducing this pressure, aided by its own musculature and by the retractor muscle, if present. In the Anopla the tenacious mucus and paralyzing secretions of the everted proboscis aid in capturing the prey, while in the Enopla the stylet is also used. Most of the Enopla have two or more pouches of accessory stylets which may replace the central stylet if lost or broken (fig. 4). In the heteronemertean *Gorgonorhynchus* the proboscis is dichotomously branched.

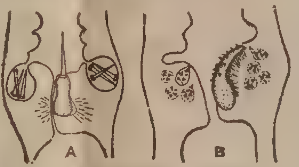


FIG. 4.—PROBOSCIS ARMATURE IN (A) AMPHIPORUS GRISEUS, A REPRESENTATIVE OF THE MONOSTYLIFERA AND IN (B) PELAGONEMERTES BRINKMANNI, A REPRESENTATIVE OF THE POLYSTYLIFERA

The *digestive system* consists of an anterior mouth which may either open ventrally posterior to the brain or terminally in connection with the proboscis opening. In the Bdellonemertea and some Hoplonemertea the mouth joins the rhynchodeum to form an atrium. The mouth leads to a slender œsophagus and thence to a more spacious stomach. The intestine continues as a straight tube, usually with numerous paired lateral diverticula, from the stomach to the rectum, which opens at the posterior end of the body (fig. 1). Some forms have a large caecum, with caecal diverticula, which extends forward from the anterior end of the intestine, while in some of the Paleonemertea and all of the Bdellonemertea there are no intestinal diverticula whatever (fig. 5). Digestion of the food materials is accomplished mainly by enzymes secreted into the stomach and intestine, although the fats are taken by phagocytosis directly into the cells of the lining epithelium. In these cells also the nutrients are stored in vacuoles until needed in the body metabolism.

The *circulatory system* consists typically of three longitudinal blood vessels, united at both ends of the body, and in most species with reservoirs, or lacunae, in the head and œsophageal region and with numerous anastomosing cross branches throughout the body.

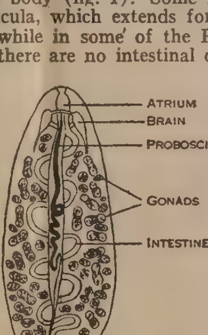


FIG. 5.—ORGAN SYSTEMS OF A BDELLONEMERTEAN

The *excretory system* is highly diversified. Typically there is a pair

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of profusely branching nephridia in close proximity with the lateral blood vessels and having one or more pairs of efferent ducts leading to the exterior of the body (fig. 1). Each of the numerous minute branches originates from a multinucleate terminal organ (metanephridium) or from a single cell (protonephridium) with long flagella which draw fluid from the surrounding parenchyma into the nephridial canal. Other cells in the walls of the canals excrete metabolized waste products. In the terrestrial nemerteans (*Geonemertes*) there are several thousand separate nephridia, each with its own efferent duct. Excretory organs have not been found in any of the bathypelagic species.

Nervous System.—The central nervous system consists of a four-lobed brain, from which a pair of large lateral nerve cords extend to the posterior end of the body. Many species have in addition a dorsomedian and a ventromedian nerve with branches communicating with the lateral nerve cords. Connected with the central nervous system are one or more pairs of proboscidial nerves and numerous, often paired, peripheral nerves associated with the muscular and digestive systems, integument, ocelli and such other sense organs as may be present.

Sense Organs.—In addition to the sensory epithelium everywhere present in the integument, some of the species have other specialized sense organs, including ocelli, cerebral, lateral and frontal sense organs, cephalic grooves and pits. In a single family (Ototyphlonemertidae) there is a pair of statocysts connected with the brain. With the exception of these organs of equilibrium and the ocelli very little experimental evidence has been obtained as to the precise nature of the sense organs. Chemical senses, including the recognition of food substances, positional sense, tactile sense and a certain degree of light sense must be located in the epithelium on all parts of the body, for headless fragments respond to the corresponding stimuli.

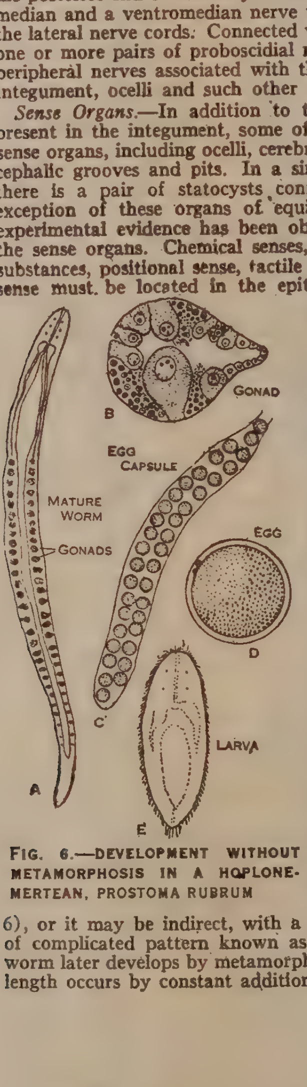

FIG. 6.—DEVELOPMENT WITHOUT METAMORPHOSIS IN A HOPLONEMERTEAN, PROSTOMA RUBRUM

Reproduction.—In most nemerteans the sexes are separate, although a few species are hermaphroditic. The gonads are simple sacs which usually alternate with the intestinal diverticula and may therefore be very numerous (figs. 1 and 6). In most species the sexual cells from each gonad are discharged directly into the water. Fertilization is thus external except for the few cases of viviparity in which the development of the embryo takes place within the body of the parent. There is evidence of sex recognition in some species, for a male and a female may be found side by side in a sheath of mucus. After ovulation and fertilization the parents leave the sheath which then forms a capsule for the developing embryos (fig. 6). In a few of the bathypelagic nemerteans the spermaries have been shifted to the head, and in the parasitic *Carcinonemertes* there is a common sperm duct which opens into the rectum.

Embryonic development may be direct, leading to the formation of a larva similar to the adult (fig. 6), or it may be indirect, with a free-swimming, hemispherical larva of complicated pattern known as the pilidium (fig. 7). The young worm later develops by metamorphosis within the pilidium. Increase in length occurs by constant additions to the posterior end of the body.

Regeneration.—Enemies are numerous, particularly annelids, crustaceans and fishes. Contributing to survival, however, is the tendency of most individuals with long bodies to break in fragments whenever any part of the body is seized. If only the posterior portion of the body is lost the missing parts are soon restored by regeneration. In certain species, any small fragment of the body, with or without the head, will regenerate into a minute worm of normal proportions (fig. 8). Fragmentation thus becomes a method of asexual propagation. Only a few species, however, have the capacity of restoring a missing head, but a lost or injured proboscis is promptly replaced.

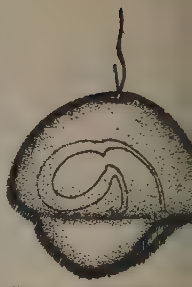

FIG. 7.—PILIDIUM OF HETERONEMERTEAN, C EBRATULUS

Classification.—Approximately 570 species of nemerteans had been described previous to 1946. Nearly 200 of these are found along the coasts of Europe, 100 on the Pacific coast of North Ameri 54 on the Atlantic coast of North America and 57 are bathypela floating far beneath the surface of the oceans.

The phylum is conveniently divided into two classes, each of wh consists of two orders.

CLASS 1. ANOPLA. Mouth posterior to brain; central nervous syst imbedded in body wall, either between the muscular layers or exter thereto; proboscis not armed with stylets.

Order 1. PALEONEMERTEA. Body musculature of either two or th layers; cutis absent. Example, P *cephalothrix* (fig. 2).

Order 2. HETERONEMERTEA. B musculature of three layers, which a thin inner circular and outer spiral layer are someti added; cutis well developed. amples, *Lineus* (fig. 8), *Cerebra lus* (fig. 3).

CLASS 2. ENOPLA. Mouth ante to brain; central nervous sys situated in parenchyma interna body musculature; proboscis cept in Bdellonemertea) ar with one or more calcareous sty

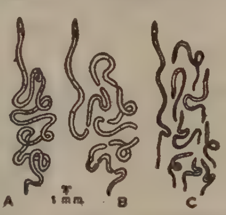

FIG. 8.—ASEXUAL REPRODUCTION BY FRAGMENTATION, LINEUS SOCIALIS

Order 3. HOPLONEMERTEA. Proboscis with armature; intes straight, with paired lateral diverticula; sucker absent

Suborder 1. Monostylifera, with single stylet on awl-shaped b Examples, *Amphiporus* (fig. 4A), *Prostoma* (fig. 6).

Suborder 2. Polystylifera, with several stylets on curved b

Tribe 1. Reptantia, adapted for creeping or burrowing.

Tribe 2. Pelagica, adapted for swimming or floating in ocean depths. Example, *Pelagonemertes* (fig. 4B).

Order 4. BDELLONEMERTEA. Proboscis without armature; intes convoluted, slender, without diverticula; with sucker at posterior of body. Commensal in marine pelecypods. Example, *Malacobd* (fig. 5).

Geographical Distribution.—Nemerteans are found along the seacoasts of the world and off the shores to depths of hund of metres. Some of the species are circumpolar, extending southw along the coasts as far as Madeira, southern New England, Califo and Japan. A few species live in both the northern and south hemispheres. Some are limited to the polar seas and others to tropics. Some of the bathypelagic species live at depths of 1,00 2,000 metres or more and the population may be carried for th sands of miles by the deep ocean currents, reproducing genera after generation in their endless circuits throughout the great oce

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Nemerteans of the Hawaiian and Marshall Islands

By WESLEY R. COE
Osborn Zoological Laboratory, Yale University, and
Scripps Institution of Oceanography, University of California[1]

NEMERTEANS OF HAWAII

It has been concluded from the reports of collectors that the nemertean fauna of the intertidal zone and off-shore waters of the Hawaiian Islands is represented by a sparse population both in numbers of species and of individuals. In my paper on "New nemerteans from Hawaii" (3)[2] only six species are mentioned, including two for which specific identification could not be made. For this reason a small collection procured from the intertidal zone at Halape, Hawaii, by Dr. Robert W. Hiatt, containing two new species is of some interest, although both are members of well-known genera. Only three species were obtained at that locality: one specimen of *Baseodiscus cingulatus* (Coe), four of *Lineus hiatti,* new species, and three of *Nemertopsis exilis,* new species.

None of the species thus far found on or near the Hawaiian Islands has been reported from any other part of the world, although all of them belong to widely distributed genera, found on the coasts of California, Japan, the Mediterranean, and elsewhere. They include three species of *Baseodiscus,* two of *Lineus* and one of *Nemertopsis,* as well as a yet unidentified species of *Drepanophorus* from the off-shore waters. A personal communication from A. E. Verrill mentions a species of *Tetrastemma* from Lihue, Kauai. This and *Baseodiscus edmondsoni* were the only nemerteans that he found in several weeks of collecting in the intertidal zone. The fact that the five genera and seven species mentioned are the only ones that have been reported from these islands presumably indicates how little attention has been devoted to the collection and identification of this group of worms. As no less than 24 genera and 69 species have already been reported from the coast of California, it seems probable that many additional species will be found on the islands.

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[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 346.

[2] Numbers in parentheses refer to Literature Cited, p. 106.

Baseodiscus cingulatus (Coe), B. P. Bishop Mus., Occ. Papers **10** (18): 6-7, 1934.

Taeniosoma cingulatum Coe, U. S. Fish Comm. Bull. **23** (3): 981-986, pl. 1, figs. 3-7, 1906.

Individuals of this species are among the most common and conspicuous of the nemerteans found on or near the islands. They are easily distinguished by their large size when fully grown and by the light-colored body with many narrow rings of reddish-brown pigment. A brown dorsal longitudinal stripe is sometimes present, but this disappears after preservation. In some individuals most of the rings encircle the body but are narrower on the ventral surface, whereas in others many of the rings are interrupted ventrally. Large individuals may exceed a meter in length and have more than 100 rings. The body is slender, usually only 1 to 4 mm. in diameter, but of such firm consistency that it is not easily broken. On each anterolateral margin of the head are 35 to 50 minute black ocelli, but these are not visible when the head is strongly contracted and the tip withdrawn into the more posterior portion of the head.

B. cingulatus was previously dredged from depths of 40 to 80 meters in the channel between Maui and Lanai, and collected near the low-water level on Oahu at Kahala, Malaekahana, and Kaaawa, and at Necker Island. One specimen was collected by Dr. Hiatt beneath a rock at the low-water level on the outer coast at Halape.

Baseodiscus edmondsoni Coe, B. P. Bishop Mus., Occ. Papers **10** (18): 3-5, fig. 1, 1934.

Body is pale yellowish or flesh color, with a broad transverse band of reddish brown on head above brain and a broad median dorsal stripe of the same brown pigment extending from posterior portion of head to posterior end of body. Transverse cephalic band is separated from main dorsal stripe by a colorless area about half as long as the width of head. Except near its anterior end the stripe is more or less interrupted at each pseudosegment by a transverse band of darker color. In some specimens the median longitudinal stripe is narrow, with 20 to 30 transverse bands of darker color extending laterally on each side. There are commonly 30 to 40 or more small black ocelli on each side of head, each group extending from tip of head to brain region, but these are not distinctly visible when head is strongly contracted.

B. edmondsoni is known only from Wake Island; from Kaaawa and Kahala, Oahu; and from Lihue, Kauai.

Baseodiscus univittatus (Coe), B. P. Bishop Mus., Occ. Papers **10** (18) : 6, fig. 2, 1934.

Taeniosoma univittatum Coe, U. S. Fish Comm., Bull. **23** : 978-981, pl. 1, figs. 1-2, 1906.

Body is pale or colorless, with a single narrow longitudinal dorsal stripe of ark reddish brown. The stripe is continuous from tip of head to posterior xtremity of body. Body is slender, reaching a length of 100 mm. or more, with diameter of only 1.5 to 3 mm.

This species was collected at the low-water level on the reefs at Kaaawa and Waikiki, Oahu, and dredged from depths of about 250 meters off the southern coast of Molokai and north of Maui.

Lineus albifrons Coe, B. P. Bishop Mus., Occ. Papers **10** (18) : 8, fig. 4, 1934.

Body is deeply pigmented anteriorly, with a sharply demarcated broad band f white on tip of head on both dorsal and ventral surfaces. The precise color f the pigment in life has not been recorded. Back of anterior third of body the igment gradually decreases and posterior half of body is much paler. Ocelli are nconspicuous or absent.

L. albifrons is known from only a single specimen collected at Kahala, Oahu. This individual measured 14 mm. in length and 1.5 mm. in diameter after preservation.

Lineus hiatti, new species.

Body slender, rounded or slightly flattened; head slender, much narrower han adjacent portion of body, pointed at extremity. Cephalic grooves long and leep. Mouth large and elongated or small and rounded, according to state of contraction; when body is strongly contracted mouth may be protruded and margins xtended to form an opening more than half diameter of body. In common with most of the other species of the genus, body is fragile and the worm usually ragments when captured.

Size: of the four specimens available for study, the largest was 4 mm. in width, 3 mm. in thickness and 100 to 150 mm. in length.

Ocelli: absent or inconspicuous.

Color: brown in life, becoming darker and almost black after preservation. Margins of cephalic grooves and extreme tip of head pale gray. Proboscis gray r pale brown.

This species is found beneath stones and matted algae near low-water level. At present it is known only from Halape, Hawaii. Types are deposited in Bishop Museum.

Individuals of this species have a superficial resemblance to those of *L. nigricans* Bürger from the Mediterranean and to *L. alborostratus*

Takakura from Japan but differ in having the head with less distinct anterior white or colorless margin.

Nemertopsis exilis, new species.

Body filiform, usually twisted and tangled, but not coiled; 20 to more than 60 mm. in length but only 0.5 to 1.5 mm. in diameter or even less when fully extended. Very firm and not easily broken. Mouth and proboscis opening united or in close contact. Proboscis sheath about one-third as long as body. Proboscis short but large in comparison with diameter of body; in some portions diameter of proboscis is more than half the width of entire body; armed with slender central stylet and slender basis, with two pouches of accessory stylets. There are 10 proboscidial nerves. Cerebral sense organs large in comparison with size of head, situated anterior to brain. Intestinal caecum ends far back of brain.

Color: one of the three specimens collected was recorded as red in life but color was entirely lost after preservation. The other two were presumably paler.

N. exilis lives beneath stones in the intertidal zone near low-water level. At present it is known only from Halape, Hawaii. Types are in the collection of Bishop Museum.

This species resembles *N. tenuis* Bürger of the Mediterranean and Atlantic coast of France but differs in character of cerebral sense organs and presumably in other anatomical details. Individuals of this species are among the most slender of all the nemerteans but the tissues are so strong that the body is not easily ruptured.

NEMERTEANS OF THE MARSHALL ISLANDS

During his investigations on the marine organisms at Bikini and Eniwetok Atolls in connection with the atomic bomb tests in the summer of 1946, Dr. Martin W. Johnson, of the Scripps Institution of Oceanography, obtained three species of nemerteans in the intertidal zone. Each of these had been reported from other Pacific islands, but the present record adds greatly to their previously known distribution. The finding of *Gorgonorhynchus* so far from its original place of discovery is of much interest. The fact that the two known species of that genus are found on opposite sides of the world justifies the conclusion that the remarkable modification of the proboscis characteristic of the genus must have been of ancient origin and not a recently acquired specialization as has been suggested by Wheeler (6).

Baseodiscus delineatus (Delle Chiaje).

Polia delineata Delle Chiaje, Animali sense Vert., Mem. **3,** Napoli, 1825.

This specimen is about 30 cm. long after preservation and 4 to 5 mm. in
ameter. The general color was dark reddish brown, consisting of about 50 fine
ngitudinal lines, alternating with an equal number of fine gray lines. This pat-
rn covers the entire body both dorsally and ventrally, with only an occasional
terruption of one of the lines. In this respect this specimen differs from the
ore common color varieties in which there is more or less complete interlacing
ıd interruption of the lines.

One individual of this widely distributed species was collected in
ıe intertidal zone at Bogoni Island, Eniwetok Lagoon.

The species has previously been reported from the Marianas and
'iji Islands and is widely distributed in both the Northern and South-
rn Hemispheres, from the Mediterranean to the Cape Verde Islands,
ɔasts of Africa, Mauritius, East Indies, West Indies, Bermuda, and
-ulf of California. The distribution of *B. curtus,* with lighter and less
ɛgular color patterns is generally coextensive with that of *B. deline-*
tus. The species which Yamaoka (7) has reported from Japan as
. curtus is obviously *B. princeps* (Coe, 1).

orgonorhynchus repens Dakin and Fordham, Nature **128**: 796, fig.
1, 1931; Zool. Soc. London, Proc. (1-2): 461-483, pls. 1-5, figs.
1-6, 1936.

Individuals of this genus differ from all other nemerteans in having the
roboscis dichotomously branched. This organ has a cephalic attachment as in
:her Heteronemertea, but the short basal portion divides into 32 or 64 branches,
ıch of which is capable of eversion like the finger of a glove. At the base of
ıch branch is a valve-like structure which allows each branch or division of
ranches to be everted separately and withdrawn again by hydrostatic pressure.
.s in some species of *Cerebratulus* and a few nemerteans of other families, the
roboscis has no retractor muscle.

One specimen of this peculiar nemertean was collected in the inter-
dal zone of the outside reef at Namu Island, Bikini Atoll.

This species was first recorded from New South Wales and later
rom tropical islands of the Great Barrier Reef. The same or a very
imilar species has been found on the coast of India. Another species,
. bermudiensis Wheeler (6) is not uncommon at Bermuda.

With the exception of the highly specialized proboscis, the genus
s similar to other genera of the family Lineidae, particularly to *Cere-*
ratulus, in anatomical features as so fully described and illustrated by
)akin and Fordham (5). Members of the genus also resemble *Cere-*
ratulus in external appearance and habits. Individuals of both genera
re adapted for swimming, although they usually remain in burrows
r hidden beneath stones.

Drepanophorus crassus (Quatrefages).

Cerebratulus crassus Quatrefages, Ann. Sci. Nat., Zool. **6**: 379-381, 1846.

One specimen measuring 68 mm. in length and 4 to 7 mm. in width, collected in the intertidal zone at Eniirikku Island, Bikini Atoll, is referred to this most widely distributed of all nemertean species. The identification cannot be positive, however, because of the absence of the proboscis. The species has previously been reported from Samoa and Tonga, as well as from the Mediterranean and other European coasts, Madeira, Mauritius, the West Indies, Panama, the west coast of Mexico, Peru, and even from shores in both the Arctic and Antarctic Oceans.

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robial Utilization of Carcinogenic rocarbons[1]

FREDERICK D. SISLER and CLAUDE E. ZOBELL
Scripps Institution of Oceanography,
University of California, La Jolla

cent investigations reveal that microorganisms of marine may be capable of decomposing carcinogenic hydro- ns associated with the production of tumors in animals. at many microorganisms possess the ability of utilizing carbons as a sole source of energy in their metabolism has previously demonstrated and confirmed (*2*). Nearly pecies of bacteria, yeasts, and molds representing 30 a have been shown to attack various hydrocarbons of the us, liquid, and solid state, and in the aliphatic, olefinic, henic, and aromatic series. Such organisms have been widely distributed in nature, from terrestrial as well as e sources. The list of hydrocarbons which have been to be subject to microbial attack is rapidly growing.

e current studies on microbial utilization of carcinogenic carbons are incidental to a comprehensive survey of the f bacteria in the decomposition and diagenesis of petro- hydrocarbons and related compounds. However, the pread interest in cancer research and the obvious need utual cooperation among all scientific workers who may ncerned, directly or indirectly, with such a vital problem ng to public health suggest that these findings be pre- d apart from those pertaining to petroleum genesis.

cluded among the compounds used as substrates were thalene, anthracene, phenanthrene, diaminobenzene, enzanthracene, and 1,2,5,6-dibenzanthracene. The two are listed in a recent survey published by the U. S. c Health Service (*1*) as having induced tumors in ex- ental animals. Like the majority of the carcinogenic ounds listed in this survey, the 6 which were investigated romatic cyclic or polycyclic hydrocarbons containing one ore benzene rings, (Fig. 1). Chemically and physically are stable and refractory compounds with low solubilities s is the case with 1,2-benzanthracene and 1,2,5,6- zanthracene, insoluble in water and the organic solvents nonly used in the laboratory.

e organisms used in the experiments were of marine n. For the purpose of demonstrating the utilization of the nogenic and related hydrocarbons by the cultures, an apparatus was employed which measured the amount of carbon dioxide evolved by the cultures upon oxidation of the substrate. Other methods for determining the rate of oxidation have been successfully used, however, including the measurement of oxygen uptake, both manometrically and by the Winkler method (*3*).

The 6 compounds tested were dispersed in ignited sand to provide suitable surface area for the organisms. Two of the compounds, 1,2-benzanthracene and 1,2,5,6-dibenzanthracene, which are solid compounds at room temperatures and insoluble in water and organic solvents, were ground to a fine powder in a mortar, which favored a more intimate contact between the organisms and the substrate. Naphthalene, anthracene, and phenanthrene were first dissolved in volatile solvents and then precipitated as a thin film on ignited sand by evaporating off the solvent.

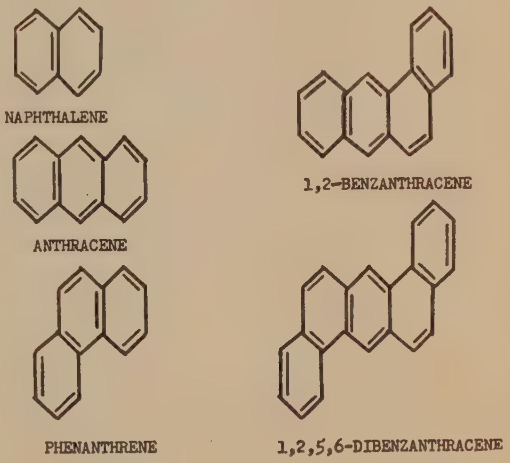

FIG. 1

After the ignited sand and substrate were added to the culture receptacles, the only additional substance used besides the inoculum was the suspension medium. For this purpose, filtered sea water containing 0.1 per cent $(NH_4)_2HPO_4$ was used. This had been previously aged for several months in the dark at a temperature favoring the removal of dissolved organic matter present. Sea water is a physiologically balanced solution and contains all the essential salts necessary to satisfy the mineral requirements of marine organisms.

The controls used in these experiments included, for the most part, those which precluded false positive readings which might result from the possible introduction of adventitious organic matter in the substrate, inoculum, suspension medium, glassware, and connections in contact with the incubating cultures, plus controls to measure endogenous metabolism. The cultures, together with 25 mg. of hydrocarbon substrate, ignited sand, and sea water, were incubated at 32° C. for four days with the controls, during which time a stream of carbon dioxide-free air was bubbled through the culture receptacles at the rate of 50 ml./minute. The carbon dioxide evolved from the oxidation of the substrate and from endogenous metabolism was collected in N/10 NaOH during the incubation period. The residual carbon dioxide remaining in the solution after incubation was driven off by acidification. The endogenous control served also to eliminate the effect of carbon dioxide (as dissolved carbon dioxide, bicarbonate, and carbonate) present in the sea water other than that evolved by metabolic processes, which would be flushed into the caustic solution upon acidification.

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[1] ntribution from the Scripps Institution of Oceanography, New 348. This paper is a contribution from the American Petroleum In- , Research Project 43A.

The carbon dioxide collected at the receiving end of the apparatus was determined by back titration. That produced by the endogenous control was subtracted from the total carbon dioxide produced by the culture acting on the substrate to give the net amount of hydrocarbon oxidized by the organisms (Table 1). Since the empirical formulas and molecular weights of the hydrocarbons under test are known, the per cent oxidation of 25 mg. of the substrate was computed.

In view of the high oxidation rates, it does not seem unlikely that a quantitative oxidation of the carcinogenic hydrocarbons could be effected with a longer incubation period.

It is not contemplated that current investigations of the microbial utilization of carcinogenic hydrocarbons will continue beyond a brief survey of those compounds of particu structural interest. The findings from these cursory inve gations have been presented with the hope of stimulat further research into the possible application of bacteria their products in the prophylactic or therapeutic treatmen cancer.

TABLE 1

AMOUNT OF CARBON DIOXIDE PRODUCED BY ACTION OF BACTERIA OI MG. OF HYDROCARBONS IN FOUR DAYS AT 32° C.

Hydrocarbon	CO_2 produced (mg.)	Amou oxidize (%)
Naphthalene	44.2	51
Anthracene	53.5	64
Phenanthrene	58.5	68
Diaminobenzene	14.0	23
1,2-Benzanthracene	41.2	47
1,2,5,6-Dibenzanthracene	11.6	13
None (Control)*	0	—

* The controls used as checks against introduction of adventitious ganic matter produced less CO_2 than the endogenous controls, hence condensed as one control shown here.

References

1. HARTWELL, J. L. Survey of compounds which have been tested carcinogenic activity. Washington, D. C.: U. S. Public Health Ser 1941.
2. ZOBELL, C. E. *Bact. Rev.*, 1946, **10**, 1.
3. ———————. *Standard methods for the examination of water sewage.* (9th ed.) New York: American Public Health Associa 1946.

Contribution No. 349

A CRITICAL WIND SPEED FOR AIR-SEA BOUNDARY PROCESSES[1]

By

WALTER H. MUNK

Scripps Institution of Oceanography
University of California
La Jolla, California

INTRODUCTION

Most processes at the air-sea boundary are modified by the existing wind pattern. In general the rate of these processes varies *gradually* with wind speed. An exception seems to occur at a wind speed of about 7 m/sec; at that speed a number of apparently unrelated processes have been observed to undergo such *abrupt* changes that, in some instances, one is led to suspect the existance of discontinuities. Not only the rate, but the very nature of these processes seems to be altered at this critical wind speed.

An explanation may be found in the Kelvin-Helmholtz instability criterion; applied to the air-sea boundary this criterion gives instability for winds exceeding 6.5 m/sec. The application involves the transition from laminar to turbulent flow, a concept fundamental to fluid mechanics. Consequently oceanographic and meteorologic processes involving the air-sea boundary can be expected to change markedly at the critical wind speed.

OBSERVATIONS OF "DISCONTINUITIES" AT BEAUFORT 4

Whitecaps. Whitecaps[2] are formed when the wind speed equals or exceeds force 4 on the Beaufort scale (Beaufort 4 includes the range 5.5–7.9 m/sec, *i. e.*, 11–16 knots). The transition from a smooth sea to a sea covered by whitecaps is so striking that it serves as one of the principal indications for judging surface winds.

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[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 349. This work represents the results of research carried out for the Hydrographic Office, the Office of Naval Research, and the Bureau of Ships of the Navy Department, under contract with the University of California.

[2] "The white froth on the crests of waves" (Knight, 1944: 829). In England the expression "white horses" is commonly used.

Reprint from SEARS FOUND. JOURN. MAR. RES.

Table I contains a description of the surface at various wind speeds. These speeds refer to average values; instantaneous values of the wind speed may exceed the average values by as much as 50%. Therefore the lowest instantaneous wind speed sufficient to bring about whitecaps appears to lie in the range 11 to 16 knots.

TABLE I. Description of Sea Surface at Various Wind Speeds

Wind Speed Beaufort	 Knots	Definition*	Description†
3	7–10	Gentle breeze	". . . produces a definite wave formation with scattered incipient whitecaps making their appearance."
4	11–16	Moderate breeze	". . . is characterized by numerous well developed whitecaps, which give the ocean a spotted appearance."
5	17–21	Fresh breeze	"The difference in the appearance of the ocean surface between forces 4 and 5 is principally one of degree. However, with force 5 spume tends to be blown from the breaking wave crests, whereas no such tendency is noticeable with force 4."

* Knight, 1944.

† U. S. Dept. of Agriculture, Weather Bureau. Instructions to marine meteorological observers, 1938.

Plates I, II and III show selected photographs of the sea surface at wind speeds just beneath and just above those required for whitecap formation. The optical properties of the sea surface differ at the two wind speeds. On vertical photographs, such as Plate III, foam patches were counted and their number over an area of approximately 10,000 square meters was plotted against the wind speed (Fig. 47). These counts depend somewhat upon personal judgment in selecting foam patches. There are no foam patches at wind speeds of less than 5 m/sec, but there are from 10 to 15 foam patches[3] for winds exceeding 7 m/sec.

Soaring of Birds. Woodcock (1940) has observed the soaring tactics of sea gulls over the open sea. He distinguishes between two types of free soaring: circle soaring, where "birds circle about in horizontally restricted, chimney-like up-drafts, being carried along downwind (if there is a wind) at the same time"; and linear soaring, where "the

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[3] Above the critical wind speed the *number* of foam patches does not increase consistently with the wind, but their diameters do increase from 3 feet for a speed of about 7 m/sec, to 25 feet for speeds exceeding 13 m/sec.

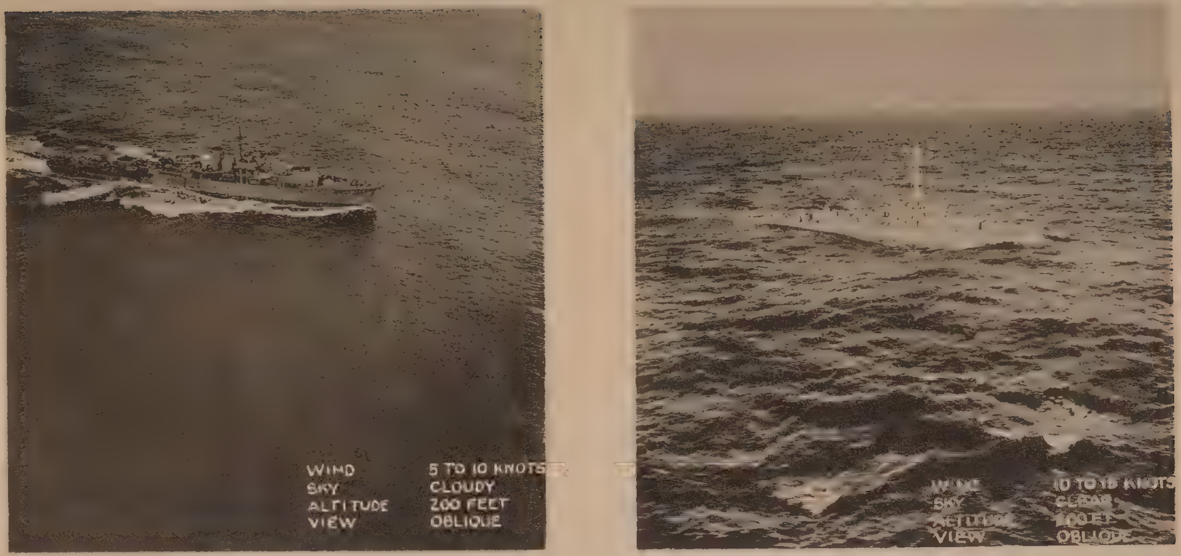
WIND
SKY
ALTITUDE
VIEW
5 TO 10 KNOTS
CLOUDY
200 FEET
OBLIQUE
WIND
SKY
ALTITUDE
VIEW
10 TO 15 KNOTS
CLEAR
OBLIQUE

Plate I. Oblique view of the sea surface from an elevation of 200 feet. The left photograph was taken during somewhat weaker winds than the right photograph, but otherwise under identical conditions. (Official Photograph, United States Navy.)

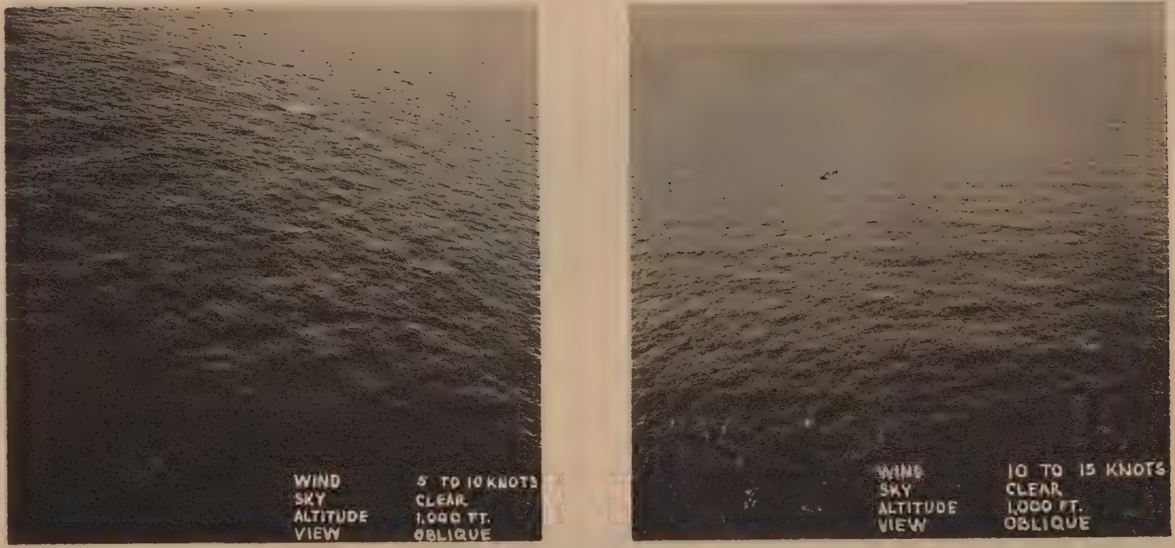
WIND 5 TO 10 KNOTS
SKY CLEAR
ALTITUDE 1,000 FT.
VIEW OBLIQUE
WIND 10 TO 15 KNOTS
SKY CLEAR
ALTITUDE 1,000 FT.
VIEW OBLIQUE

Plate II. Oblique view of the sea surface from an elevation of 1000 feet. The left photograph was taken during somewhat weaker winds than the right photograph, but otherwise under identical conditions. (Official Photograph, United States Navy.)

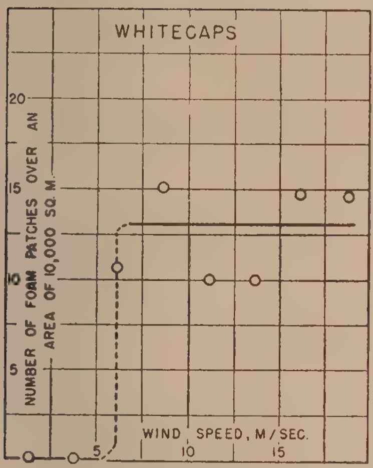

Figure 47. Foam patches are observed only for wind speeds exceding 7 m/sec.

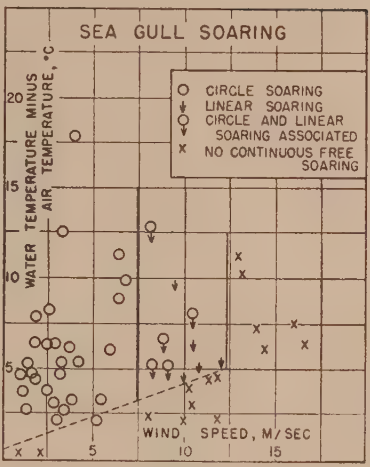

Figure 48. Observations of soaring sea gulls reveal a change in tactics at a wind speed of about 7 m/sec. This is believed to be the result of changes in the convection pattern above the sea surface. After Woodcock (1940).

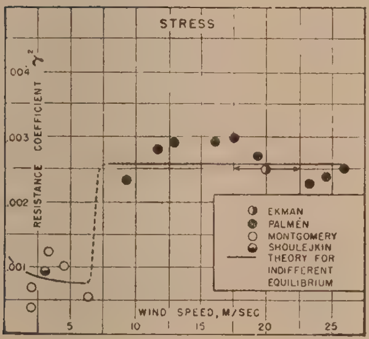

Figure 49. Observations of storm tides and of the vertical wind profile over the ocean reveal a sharp change in the resistance coefficient at a wind speed of about 7 m/sec. Arrows to both sides of Ekman's observation indicate range of wind speeds over which observation is applicable.

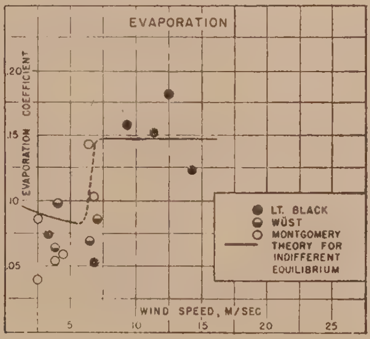

Figure 50. Observations of the humidity gradient above the sea indicate a sharp change in the evaporation coefficient at a wind speed of about 7 m/sec. After Sverdrup (1946).

birds move in a line directly against the wind flow." Observations of soaring during periods when sea temperature exceeded air temperature[4] have been plotted on Fig. 48; each of these 53 observations extended intermittently over an average time interval of six hours. For winds above 7 m/sec there is both circle-soaring and linear-soaring. According to Woodcock, "there is no linear soaring below 7 meters per second."

Resistance Coefficient. Taylor (1916) has defined a dimensionless parameter, the resistance coefficient γ^2, by the equation

$$\gamma^2 = \tau/\rho' U^2, \tag{1}$$

where ρ' is the density of air, U the wind speed at an elevation of approximately 15 meters above sea level, and τ the mechanical stress exerted by the wind on the sea surface. Stress cannot be measured directly but may be computed from indirect evidence. Ekman (Sverdrup, *et al.*, 1942: 490) computed stress from measurements of sea level rise during a storm in the Baltic (storm tides). Palmén and Laurila (1938) made a similar study, dealing with the effect of wind on sea level in the Gulf of Bothnia, wind speeds ranging from 9 m/sec to 26 m/sec. Within this range γ^2 appears to have a constant value of about 0.0026 (Fig. 49), so that the stress equals

$$\tau = 2.6 \times 10^{-3} \rho' U^2. \tag{2}$$

The implications of this relationship, in the light of similar "quadratic laws" for the flow of fluids over *rough* plates, have been discussed by Rossby and Montgomery (1935) and will be dealt with later. Further evidence in favour of a constant value of γ^2 for winds exceeding 6 to 8 m/sec can be found in the successful application of equation (2) to such oceanographic processes as upwelling along the coast of southern California (Sverdrup and Fleming, 1941), the generation of waves by wind action (Sverdrup and Munk, 1947), and the maintenance of equatorial currents by wind stress (Sverdrup, in press).

At low wind speeds the empirical data are much less conclusive. Rossby has found Von Kármán's equation for the flow of fluids over *smooth* plates in agreement with observations by Montgomery and by Shoulejkin of the wind profile above the sea (Rossby, 1936: fig. 1). Stress can be computed from simultaneous measurements of wind speed at two levels according to the equation

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[4] In cases where the air temperature exceeds the water temperature, factors related to the stability in the lowest air layers tend to obscure the transition at the critical wind speed.

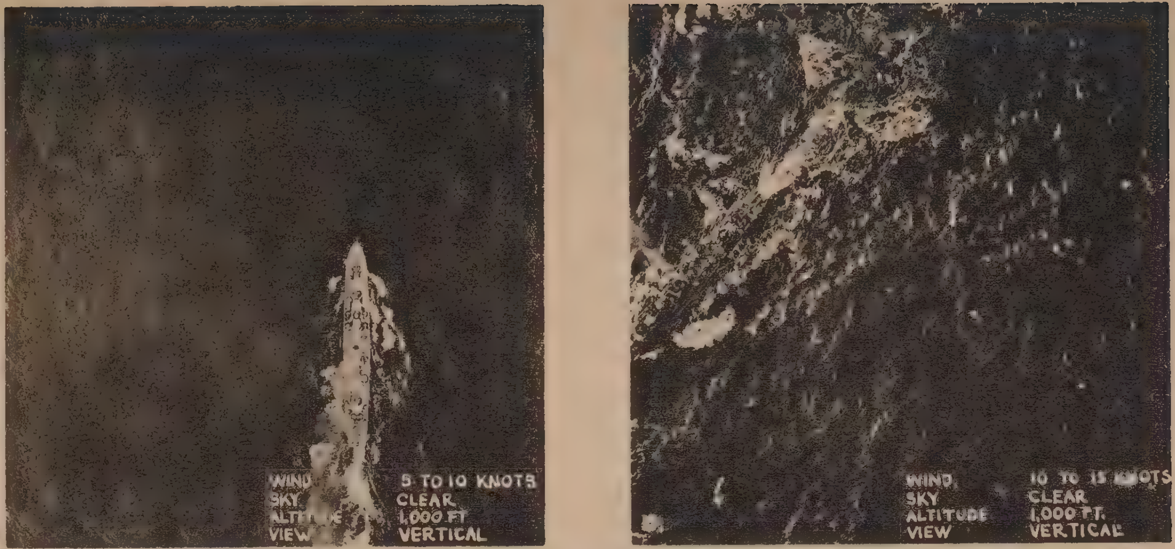
WIND 5 TO 10 KNOTS
SKY CLEAR
ALTITUDE 1,000 FT
VIEW VERTICAL
WIND 10 TO 15 KNOTS
SKY CLEAR
ALTITUDE 1,000 FT.
VIEW VERTICAL

Plate III. Vertical view of the sea surface from an elevation of 1000 feet. The left photograph was taken during somewhat weaker winds than the right photograph, but otherwise under identical conditions. (Official Photograph, United States Navy.)

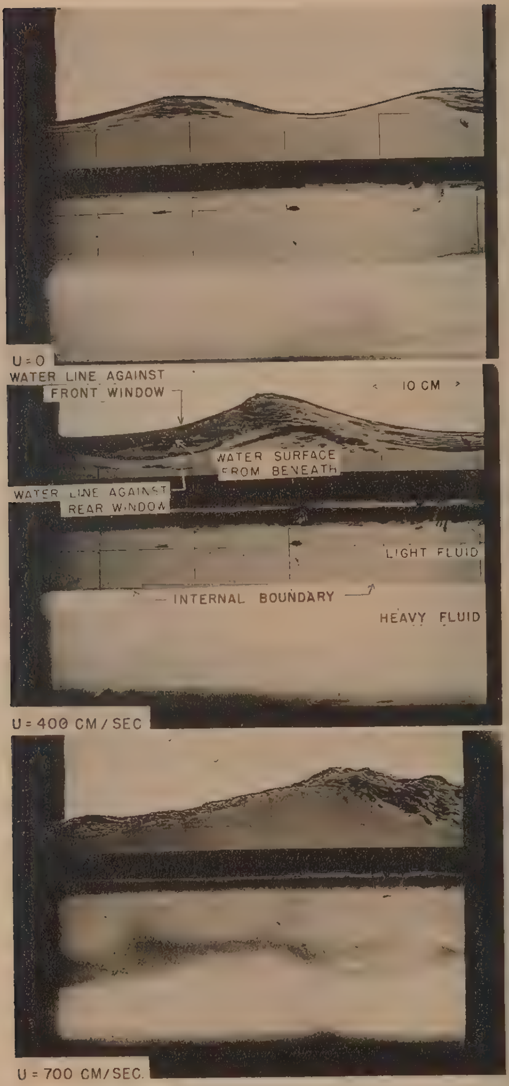
U = 0
WATER LINE AGAINST FRONT WINDOW
10 CM
WATER SURFACE FROM BENEATH
WATER LINE AGAINST REAR WINDOW
LIGHT FLUID
INTERNAL BOUNDARY
HEAVY FLUID
U = 400 CM / SEC
U = 700 CM / SEC.

Plate IV. Effect of wind on waves generated mechanically in an experimental tank. The camera was beneath the level of the water surface outside the tank, so that the boundary is seen from below. For a wind of 700 cm/sec (bottom photograph) the water surface is rough and eddies form at the internal boundary.

$$\sqrt{\tau/\rho'} = \frac{k\,(U_2 - U_1)}{\ln\,(z_2/z_1)}, \tag{3}$$

where $k = 0.4$, U_1 and U_2 are the wind speeds at elevations z_1 and z_2, respectively. Values of the resistance coefficient for low wind speeds have been computed from these observations and plotted in Fig, 49. All wind speeds have been adjusted to an elevation of 15 meters by means of the equation

$$\frac{U_{15} - U_1}{\ln\,(z_{15} - z_1)} = \frac{U_2 - U_1}{\ln\,(z_2/z_1)}. \tag{4}$$

Montgomery's observations were made simultaneously at two levels, Shoulejkin's observations at four different levels. The solid curve segments in Fig. 49 refer to Rossby's equations for the stress over smooth and rough surfaces.

Evaporation Coefficient. Montgomery (1940) has defined another dimensionless parameter, the evaporation coefficient, by the equation

$$\Gamma = -\frac{1}{e_s - e_a}\,\frac{de}{d\ln z}, \tag{5}$$

where e is the vapor pressure at an elevation z above the sea surface, e_s the vapor pressure at the sea surface, and e_a the vapor pressure at a standard level above the sea surface.

Sverdrup (1946) has discussed the relationship between wind speed and the humidity gradient over the sea surface, and he finds that for indifferent equilibrium conditions the evaporation coefficient changes abruptly from a value of .08 to almost .15 at a wind speed of about 6 m/sec. His striking graph is reproduced in Fig. 50. The solid curve segments show the theoretical relationships for smooth and rough surfaces.

Laboratory Measurements. Plate IV shows three photographs taken during laboratory measurements conducted at the Institute of Hydraulic Research, University of Iowa, by Dr. H. Rouse and the author. Waves were generated by a plunger at one end of a flume and wind blown over the water surface.

The three photographs show the wave motion at gradually increasing wind speeds. By using two layers of fluid of different color and density, the water motion beneath the surface can be studied. No appreciable mixing across the internal boundary can be noted until the surface wave breaks; thereupon the laminar flow pattern is disturbed and eddies are formed at the internal boundary. Thus the effect of the critical wind speed is not confined to the sea surface and to the layers directly above and beneath the surface, but appears to make itself felt at greater depths. The laboratory measurements are summarized in Table II.

TABLE II. Results of Laboratory Measurements

Mean wind speed, U_{mean}, in m/sec	Above 4.5	Below 4.5
Wind speed above crests, U_{crest}, in m/sec ($U_{\text{crest}} = 1.4\ U_{\text{mean}}$)	Above 6.3	Below 6.3
Number of runs during which crests broke	10	1
Number of runs during which no breaking occurred	3	15

The wind speed U_{mean} refers to a mean water level 14 cm beneath the top of the flume. The elevation of the average breaking crest above the mean level equalled 4 cm, so that the thickness of the air layer above the crests equalled 10 cm. According to Bernoulli's principle the product of the thickness of the air layer with the air speed must remain constant and the air speed directly above the crests, U_{crest}, must equal 1.4 U_{mean}. According to Table II, breaking occurred in 77% of the runs for which the wind speed above the crests exceeded 6.3 m/sec; and in 6% of the runs for which the wind speed was less than 6.3 m/sec.

Other Observations. Langmuir's (1938) careful measurements on Lake George imply a distinct change in the convection pattern at wind speeds somewhere between 4 and 8 m/sec for indifferent equilibrium conditions. A similar change in the convection pattern is reflected in the vertical distribution of temperature and salinity in the upper layer of the ocean (Armstrong, 1947). Another indication of discontinuity is the marked change in "sea return" on radar screens at a wind speed of about 7 m/sec. Also the general noise level in the sea and the reverberation from the sea surface are affected though not apparently to an equally marked degree.

The transition from a stable to an unstable sea surface is likely to have important bearing upon the capacity of the sea surface to reflect light and other radiation; it may affect still other processes. Observations should be planned and their analyses carried out to allow for a discontinuity at Beaufort 4.

THE TURBULENCE MODEL BY ROSSBY AND MONTGOMERY

From wind observations over the ocean, Rossby and Montgomery (1935), Rossby (1936), have inferred the existence of two hydrodynamically distinct types of sea surfaces. In order to account for the profile observed at low wind speeds, Rossby assumes a 'hydrodynamically smooth' surface with a very thin (about 1 mm) laminar boundary layer directly above it. For winds exceeding a certain critical value, Rossby and Montgomery assume the sea surface as 'hydrodynamically rough' with turbulence extending to the very surface. The authors do not state the critical wind speed explicitly, but their discussion implies a value somewhere between 6 and 8 m/sec at indifferent stratification.

In this manner Rossby has been able to account for the difference in stress at low and high wind speeds; indeed the data shown in Fig. 49 contains some of the evidence used to establish the concepts of smooth and rough sea surfaces. Sverdrup (1946) has used the Rossby-Montgomery model to account theoretically for the abrupt change in evaporation at a wind speed of about 7 m/sec (Fig. 50). Woodcock (1940) follows similar reasoning to explain the change in soaring tactics of sea gulls.[5] Also, it seems likely that white caps, breaking waves in tanks, convection patterns above and beneath the sea surface, radar "sea return," and noise level in the ocean, are all related (directly or indirectly) to the hydrodynamic character of the sea surface.

The laws applied by Rossby and Montgomery to the wind profile over the sea surface are identical with laws established in laboratory experiments dealing with the flow of fluids over plates. At low wind speeds air flow over the ocean is analogous to flow of fluids over smooth plates; at high wind speeds it is analogous to flow over plates which have been artificially roughened by means of sand grains. In view of these analogies the concepts of a hydrodynamically smooth and hydrodynamically rough sea surface were introduced. However, these laboratory experiments provide no basis for assuming that the sea surface can have the characteristics of *either* a rough or a smooth surface, depending upon the wind speed. A possible basis for assuming the curious dual role of the sea surface is presented in the next section.

THE INSTABILITY CRITERION

Two fluids, of densities ρ and ρ', are separated by a sharp boundary (Fig. 51). The ratio s of the upper density to the lower density is assumed to be less than one. Let C, L, and H denote the speed,

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[5] "There is some evidence that the force exerted by the wind on the sea surface cannot be expressed by a single continuous function of wind velocity and other factors, so that the critical values of these factors are also of interest to oceanographers. The soaring gulls seem to provide some clues as to the critical wind speeds at which there are marked changes in the form of convective motion, and thus in the transfer of momentum between the two mediums."

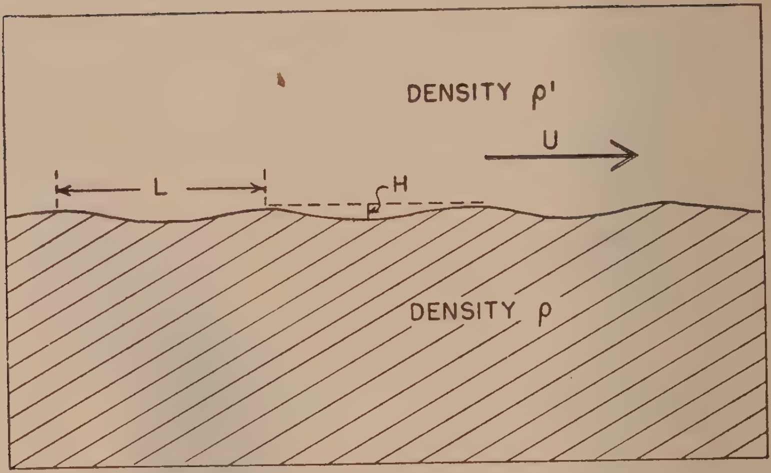

Figure 51. A fluid of density ρ' is separated by a sharp boundary from a fluid of density ρ. The upper fluid moves relative to the lower fluid with a uniform speed U. Waves at the boundary between the fluids have a height H, a length L.

length and height of waves formed at the interface in the absence of currents. If the upper fluid is moving with a speed U relative to the lower fluid, then to any particular value of the wave velocity C there corresponds a critical fluid speed, $U = U'$ (Lamb, 1932; 373–374):

$$U' = C\left[\frac{1+s}{\sqrt{s}}\right]. \tag{6}$$

For $U < U'$ waves gradually diminish in height until they die out; for $U > U'$ waves grow according to the equation

$$H = \text{constant } e^{\alpha t}, \tag{7}$$

where

$$\alpha = \frac{2\pi}{L}\sqrt{\left[\frac{s}{(1+s)^2}\right]U^2 - C^2}, \tag{8}$$

until the height becomes so large that certain assumptions underlying the foregoing equations are transcended.

This instability criterion was established by Helmholtz (1868), who attempted to explain cyclonic disturbances at a surface separating cold and warm air. Applied to the air-sea boundary, the criterion shows that for any value of the wind speed, no matter how small, certain waves will grow, provided their velocity is sufficiently small.

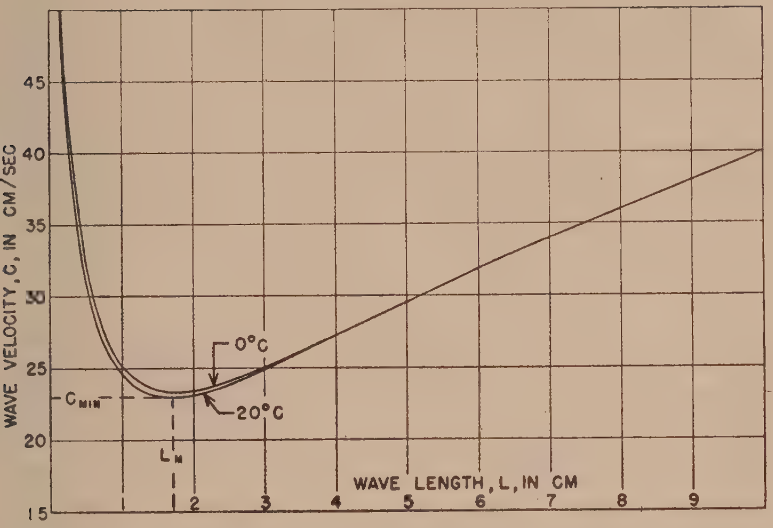

Figure 52. Wave velocity as function of wave length for two values of water temperature. The wave velocity has a minimum value, due to the opposing effects of gravity and surface tension.

Lord Kelvin (Thomson, 1871) has shown, however, that due to the effect of surface tension (σ), the wave velocity must always exceed a minimum value[6] as shown in Fig. 52:

$$C_{\min} = \left[\frac{1-s}{(1+s)^2} \frac{4g\sigma}{\rho} \right]^{1/4}. \tag{9}$$

The length of the waves of minimum velocity equals

$$L_m = \frac{2\pi}{\sqrt{1-s}} \sqrt{\frac{\sigma}{g\rho}}. \tag{10}$$

The general relationship between wave velocity and length becomes particularly simple in terms of the minimum values (Lamb, 1932: 459):

$$\frac{C}{C_{\min}} = \sqrt{\frac{1}{2}\left(\frac{L}{L_m} + \frac{L_m}{L}\right)}. \tag{11}$$

Fig. 52 shows the relationship between C and L for two extreme values of temperature:

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[6] Lord Kelvin, during a boatride in the sound of Mull, which he undertook jointly with Helmholtz, was also the first to confirm the theoretically derived value for the minimum wave valocity.

Application of equation (6) to the special case of waves of minimum velocity leads to the definition of a critical wind speed, U_c,

$$U_c = C_{\min}\left[\frac{1+s}{\sqrt{s}}\right]. \tag{12}$$

For $U < U_c$ the sea surface is stable for waves of all lengths and periods. Some numerical values are given in Table III.

TABLE III. Numerical Values of Minimum Wave Velocities and Critical Wind Speeds

$\rho' = 1.25 \times 10^{-3}$ g/cm³
$\rho = 1.025$ g/cm³
$s = 1.22 \times 10^{-3}$
Salinity $S = 33$°/oo

Water temperature	32° F (0° C)	68° F (20° C)
Surface tension* σ (g/sec²)	76.4	73.5
$C_{\min}$ (cm/sec) (equation 9)	23.3	23.0
L_m (cm) (equation 10)	1.73	1.69
U_c (cm/sec) (equation 11)	668.0	658.0
U_c (knots)	13.0	12.8

* $\sigma = 75.64 - 0.144\,\vartheta$ (° C) $- 0.0221\,S$ (°/oo), (Sverdrup, *et al.*, 1942: 70).

The critical speed U_c equals about 660 cm/sec, or 13 knots, and varies only slightly with temperature. This numerical value has been quoted in a number of investigations (Thomson, 1871; Jeffreys, 1925; Thorade, 1931: 42; Lamb, 1932: 462), but no further significance has been attached to it, as all these investigations were concerned with the lowest wind capable of raising waves. According to Jeffreys (1925) ". . . the velocity of a wind just strong enough to raise waves is actually only about 110 cm/sec . . .".

The derivation of the critical speed assumes a sharp break at the boundary. Although gusts from elevations of 15–30 feet may occasionally penetrate the lowest air layers and reach the sea surface without having lost a large fraction of their momentum, the *mean* wind speed undergoes a continuous, though a rapid, change in the region directly above the sea surface. Attempts to extend the Kelvin-Helmholtz analysis to a velocity profile which does not assume a sharp break at the boundary have met with great difficulties.

The profile of the mean wind and the amount of turbulence in the air depend upon the temperature gradient in the lower air layer. During typical summer conditions the water cools the air from beneath and the air is horizontally stratified. During winter the water is likely to be warmer than the air, so that convection and turbulence stirs the lower air layers. Assuming the wind to be measured at a fixed elevation, it follows that instability of the sea surface is attained at lower wind speeds during the winter than during the summer. If whitecaps can be related to instability of the surface, this would explain the common observation that whitecaps are formed at lower wind speeds during the winter than during the summer. Compared to the effect on boundary stability of the temperature gradient in the air, any variations in surface tension or density due to the absolute variations in temperature are negligible (Table III).

DISCUSSION AND CONCLUSIONS

A clear distinction must be made between wind waves and unstable wavelets. The dimensions of wind waves are many times the dimensions of the wavelets; furthermore, wind waves can be formed by winds of only 110 cm/sec, whereas wavelets require winds exceeding 660 cm/sec. During wind speeds between 110 and 660 cm/sec the sea surface is a hydrodynamically smooth surface, but it is not a *plane* surface. Small, smooth and stable wind waves are present. In addition, occasional gusts ruffle the surface, but the small corrugations are almost immediately smoothed under the action of surface tension. Once the wind speed exceeds the critical value, these corrugations not only persist, but also grow rapidly.

Direct observation of these wavelets is difficult because of their minute size. According to Table III their length at the critical wind speed is less than 2 cm. Careful observations indicate the existence of such very small corrugations; occasionally they appear to break and leave behind a tiny trail of bubbles. The wavelets, although too small to account directly for such conspicuous features as whitecaps, may be responsible for determining the characteristic roughness of the sea surface. Table IV gives the maximum dimensions of the wavelets according to equations (6) and (11), assuming the height of the wavelets to equal between 1/3 and 1/2 their length.

TABLE IV. Dimensions of Unstable Wavelets at Various Wind Speeds According to the Kelvin-Helmholtz Theory

U' (m/sec)	L (cm)	H (cm)
6.61	1.71	0.7
10.0	7.5	3.0
15.0	17.7	7.0
20.0	31.4	12.6
30.0	71.0	28.4

According to Rossby (1936: 19), "the roughness parameter (of the sea surface) corresponding to steady moderate to strong winds seems to be in the vicinity of 0.6 cm. . . .," and within this range does not change markedly with wind speed. The average height of the unstable wavelets in the range of wind speeds between 10 and 20 m/sec is 11 cm, or roughly 20 times the roughness parameter. This factor lies intermediate between a factor of 30 suggested by Prandtl (1932) on the basis of wind tunnel experiments using sand grains for roughness and a factor of 10 determined by Sverdrup (1936) from measurements of wind over a snow field. Although the computed dimensions of the wavelets do not meet Rossby's requirement of being independent of wind speed, it may be significant that they are of the order of magnitude suggested by Rossby. In all events it is considered significant that *the Kelvin-Helmholtz theory gives instability at a wind speed which corresponds, within the limits of observational error, to the critical speed for transition from a hydrodynamically smooth to a hydrodynamically rough sea surface.*

The manner in which stability or instability bears upon turbulence and other processes at the air-sea boundary is only conjecturable, but so are any of the other causes of turbulence. Most of our knowledge is based upon the investigations by Rayleigh and Kelvin (Lamb, 1932: 670–674) into the stability of infinitely small disturbances superimposed upon flow through pipes and channels. In analogy with these investigations it may be reasoned that instability at the sea surface is the *cause* of turbulence at the boundary. From this point of view the Kelvin-Helmholtz criterion can be interpreted in terms of a nondimensional number, $U\sqrt{s}/C_{\min}\,(1+s)$; a value of "one" marks the transition from laminar to turbulent flow at the boundary, just as a Reynolds number of 2000 marks the transition from laminar to turbulent flow in pipes.

The analogy may be carried further, and the pattern in the air flow over the wave crests compared to the flow of fluids around cylinders (Figs. 53, 54). As long as the flow is laminar the stream lines follow the entire wave profile, and the resultant force on the wave profile is zero (Lamb, 1932: 77). When irregular turbulent flow has set in the pressure against the wave profile is proportional to the square of the wind speed; the air flow spearates from the sea surface shortly to the lee of each crest and impinges upon the windward side of the next crest. A negative pressure or suction is likely to be found near the point of separation. An eddy is formed to the lee of each crest. The roughening of the sea surface permits the wind to grip the water and to apply greater tangential stress.

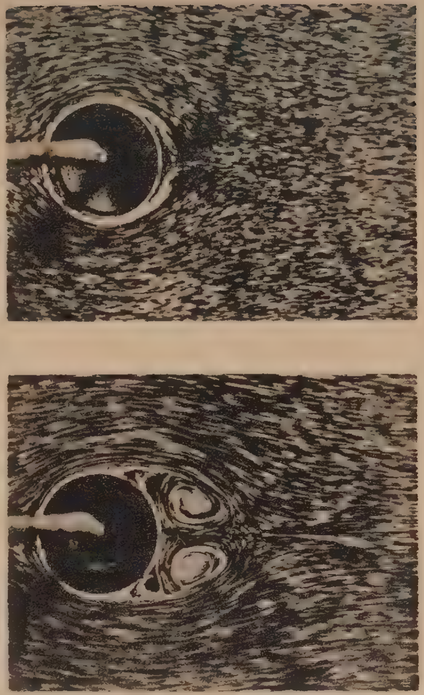

Figure 53. Observed flow of fluid past a cylindrical obstacle. Top figure: low speed; bottom figure: high speed. After Goldstein (1938: I 63).

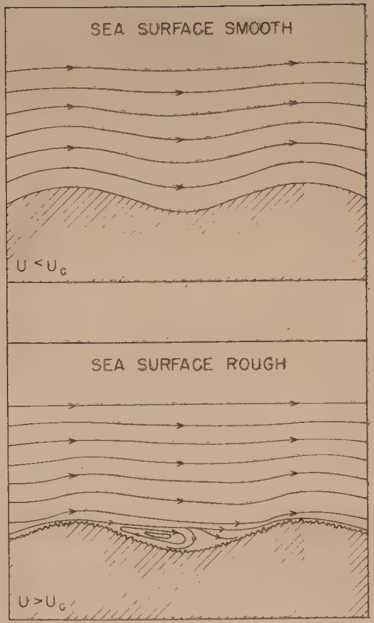
SEA SURFACE SMOOTH
U < U_c
SEA SURFACE ROUGH
U > U_c

Figure 54. Assumed flow of air over waves. Top figure: less than critical speed; bottom figure: greater than critical speed.

The growth of surface waves, due to the combined action of wind pressure against the wave profile and tangential stress along the sea surface (Sverdrup and Munk, 1947: 9–12), would be accelerated by all these factors. Presumably this acceleration accounts for incipient whitecaps at wind speeds slightly in excess of the critical speed. Therefore the appearance of whitecaps is interpreted as the most direct visual evidence of the transition to instability. It is not difficult to see that other boundary processes would be affected materially at this point.

Two related problems, one the breaking of waves in the open sea during winds much higher than the critical speed, the other dealing with the initial formation of waves during winds much less than the critical speed, go beyond the scope of this paper and hence can be mentioned only briefly. The first problem concerns interference between wave trains; in that connection Unna (1941) has pointed out that the converging flow pattern in front of the crests of waves must lead to an effective steepening of small waves overriding the main wave system. The second problem has been treated by Jeffreys (1925) on the premise that for a wind speed of 110 cm/sec (the lowest wind capable of raising waves) the rate at which energy is supplied by normal wind pressure must equal the rate at which energy is dissipated by molecular viscosity. In assuming the normal pressure proportional to the square of the wind speed, Jeffreys implies fully developed turbulence at winds of 110 cm/sec, in contrast to the evidence presented in this report. Furthermore, Jeffreys obtains a value for the "sheltering coefficient" which is more than twenty times the value obtained by Sverdrup and Munk (1947: 22) from observations of the rate of growth of wind waves. The problem of initial wave formation therefore deserves further consideration.

The author is indebted to Dr. H. U. Sverdrup, Mr. R. S. Arthur and Mr. D. F. Leipper for suggestions and criticism.

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Contribution No. 350

Contributions from the Scripps
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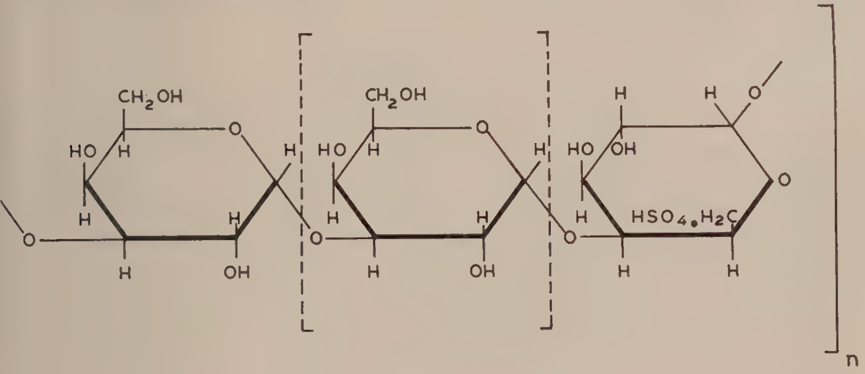
AGAR

Agar is a seaweed colloid (phycocolloid) extracted from *Gelidium* and ot agarophytes, all belonging to the red algae (Rhodophyta). It is amorphous, a comes on the market as powder, flakes, rectangular blocks, and in bundles of slen strips. It is porous, translucent, membranous, faintly yellowish, brittle when c and tough when damp. Agar is also known as agar-agar, the word being Mala in origin. In Japan, it is called "kanten." Its many synonyms, as appear on European markets, include "Chinese moss," "seaweed isinglass," "Chinese i glass," "Japanese isinglass," "Chinese gelatin," and "Japanese gelatin." See a *Seaweed colloids.*

In the form of a sweetened and sometimes flavored gel, agar has been used a dessert by the Orientals for ages. In its dried form, agar has been known since middle of the 17th century, when the process of purifying and drying agar in present form was accidentally discovered by an innkeeper in Japan. Agar introduced from China into Europe and America in the middle of the last centur serve primarily as a gelatin substitute for making the jelly type of desserts. idea of using agar as a solid bacteriological culture medium was first conceived b German housewife, Frau Fanny Eilshemius Hesse, and tried successfully by husband, a doctor. The discovery was passed to Robert Koch, who used this t unusual substance as the culture medium for his famous experiments on tubercul bacteria. In his now classical preliminary note on the tubercle bacillus publis in 1882, Koch formally announced agar as a new solid culture medium. Since th agar has become an indispensable substance in microbiological and public hea laboratories (see *Microorganisms*), and an important colloid in food and ot industries.

Chemical Nature

Agar is the sulfuric ester of a linear galactan. It consists of a long chain of D- topyranose residues, attached by 1,3-glycosidic linkages. This chain is termi- l at the reducing end by one residue of L-galactopyranose. Attached to the rest e chain through carbon atom 4, this L-galactose residue is esterified at carbon 6 with sulfuric acid. There are probably as many as 53 galactose units to SO_4H group, and at least 140 such units to each nonreducing end group. The itution of the agar molecule may be represented by the following formula, as osed by Jones and Peat (1942):



Agar

In the natural state, agar occurs as a cell wall constituent of the agarophytes, ably existing in the form of its calcium salt or a mixture of calcium and mag- im salts.

Properties and Reactions

Agar is insoluble in cold water, but swells considerably, absorbing as much as ty times its own weight of water. It dissolves readily in boiling water, and to a firm gel at concentrations as low as 0.5%. In its gelling power, agar is tanding among the colloids. Although a 1% agar sol solidifies at about 40°C., el does not melt until warmed to about 95°C., thus exhibiting a striking case of eresis.

A 1% agar sol at neutrality has a viscosity of 1.26 relative to water, when sured by an Ostwald viscometer at 45°C. An agar sol is slightly negatively ged. Its stability depends upon two factors, hydration and electric charge, emoval of both of which will result in flocculation of the agar. Agar gels, like r gels, exhibit the phenomenon of syneresis, shrinking and exuding some liquid their surfaces upon standing. Agar from different sources shows different ees of syneresis.

Upon hydrolysis with 1% sulfuric acid solution, agar yields galactose, which re- s Fehling's solution. This distinguishes it from gelatin and isinglass, which it nbles in certain respects. Both gelatin and isinglass yield ammonia when heated soda lime, whereas agar does not. Like gelatin, a cold solution of agar gives a pitate with tannic acid. With thionine blue, agar gives a characteristic violet while gelatin develops a bluish shade.

Sources

The principal sources of agar are plants of the algal genus *Gelidium*. Th are gathered from Japanese, Chinese, Californian, and Lower Californian wat Since these plants grow most abundantly on rocks in water ten to forty or more deep, they have to be harvested by diving and hand-picking. Other impor sources of agar are the red seaweeds *Ahnfeltia* from Sakhalin, Siberia, and the W Sea coast, *Pterocladia* from New Zealand, and *Gracilaria* from Australia, So Africa, and North Carolina and Florida in the United States. There are more t forty species of red algae used as secondary and supplementary raw material the manufacture of agar.

Manufacture

PRINCIPLE OF MANUFACTURE

Commercial preparation of agar is based on the principle that it is solub hot but relatively insoluble in cold water. Agar is therefore extracted by bo the agarophyte in water. The resulting liquor is filtered, and the filtrate coole form a gel, which is then cut or chopped in whatever form is desired. The cu chopped gel is frozen by natural or artificial means, and the frozen mass thawe free agar from salts and various impurities which are soluble in cold water. wet agar may be repeatedly washed with cold water, and is finally dried in the su by artificial heat. The product may be quite colorless if the agarophytes are bleached prior to the processing. If not, bleaching with a suitable agent, suc sodium hypochlorite, may be effected while the agar is still wet.

JAPANESE PROCESS

The original Japanese process depends entirely upon natural means and is employed by the majority of Japanese agar firms. The agarophytes are gene cleaned and bleached before they are subjected to the extraction process. They boiled with about fifty times their weight of water in an iron kettle. After abo to 6 hours' boiling with frequent stirring, one part of sulfuric acid or ten par vinegar per thousand parts of the agarophytes is introduced to hasten digestion. Boiling is continued for another half hour. The hot liquor is fil through cloth and the filtered liquor collected in a large vat, then ladled o wooden trays to gel. The jelly is cut into the desired shape, spread out on ba mats or on boards placed on elevated trestles outdoors. Complete freezing gene requires from 2 to 3 nights. Water crystallizes out during the freezing, and, the frozen gel thaws, water runs out carrying with it the salts and other so impurities, thus leaving the agar in relatively pure condition. After thawing agar is left to dry in the sun.

AMERICAN PROCESS

In America (see Fig. 1) artificial means are utilized as extensively as pos The sun-dried, unbleached *Gelidium* is thoroughly washed and soaked for 12 hours. The ratio of fresh water added to the agarophyte is largely dependent its quality—usually one gallon per pound of seaweed. The washed and so *Gelidium* is transferred to pressure cookers and heated by steam at a pressu

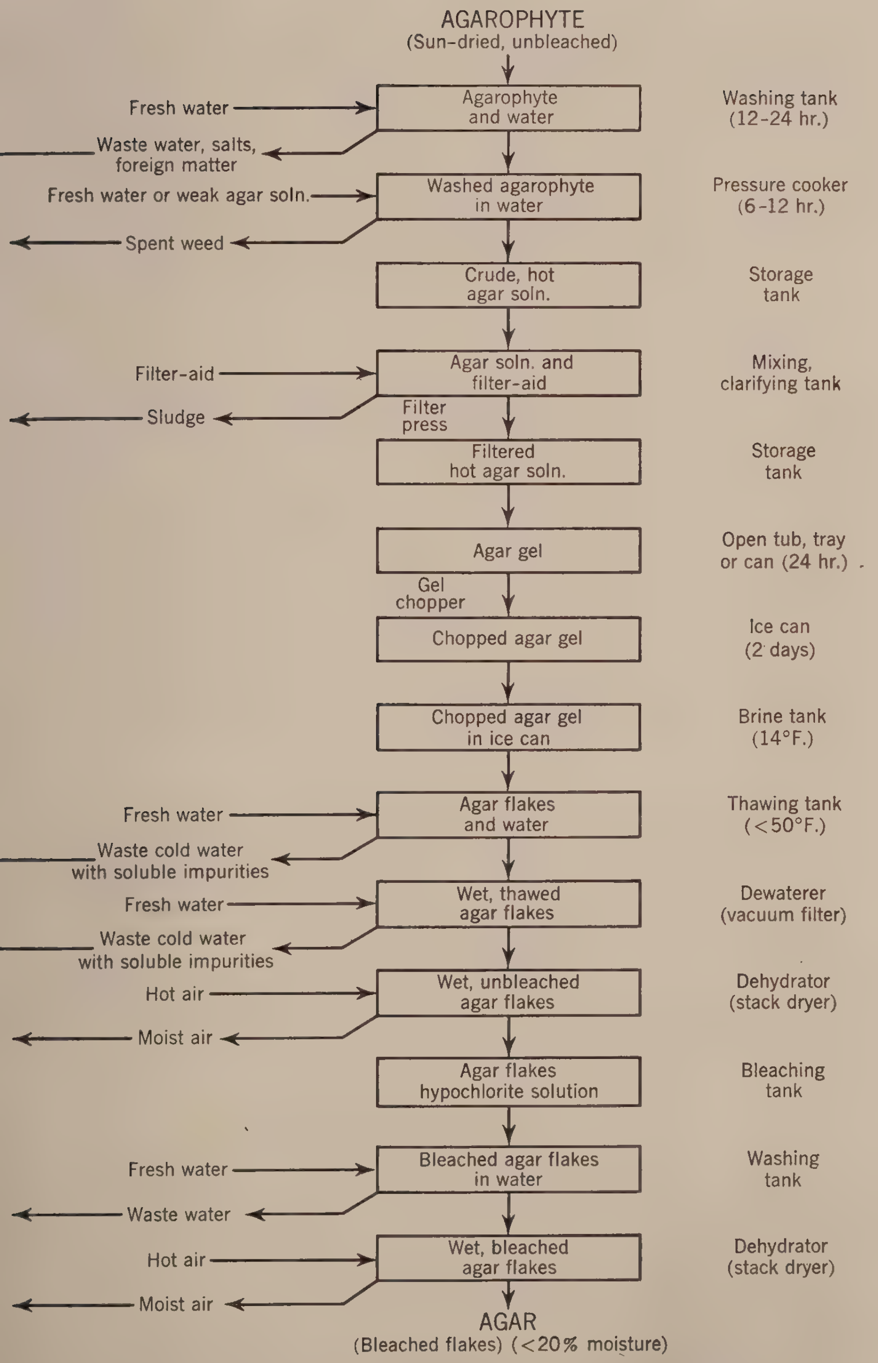

AGAROPHYTE
(Sun-dried, unbleached)
Fresh water
Agarophyte and water
Washing tank (12-24 hr.)
Waste water, salts, foreign matter
Fresh water or weak agar soln.
Washed agarophyte in water
Pressure cooker (6-12 hr.)
Spent weed
Crude, hot agar soln.
Storage tank
Filter-aid
Agar soln. and filter-aid
Mixing, clarifying tank
Sludge
Filter press
Filtered hot agar soln.
Storage tank
Agar gel
Open tub, tray or can (24 hr.)
Gel chopper
Chopped agar gel
Ice can (2 days)
Chopped agar gel in ice can
Brine tank (14°F.)
Fresh water
Agar flakes and water
Thawing tank (<50°F.)
Waste cold water with soluble impurities
Fresh water
Wet, thawed agar flakes
Dewaterer (vacuum filter)
Waste cold water with soluble impurities
Hot air
Wet, unbleached agar flakes
Dehydrator (stack dryer)
Moist air
Agar flakes hypochlorite solution
Bleaching tank
Fresh water
Bleached agar flakes in water
Washing tank
Waste water
Hot air
Wet, bleached agar flakes
Dehydrator (stack dryer)
Moist air
AGAR
(Bleached flakes) (<20% moisture)

Fig. 1. **American process of agar manufacture — plant flow sheet diagram** (4).

about 15 p.s.i. The first cooking lasts for about 6 hours. The partly spent seawee then receives two more extractions, 8 and 12 hours respectively, before being di carded. The third extract is usually very low in agar content, and is used cooking fresh material.

The extract is clarified with a filter-aid and forced through an ordinary filt press. The clear liquor is then poured into open tubs and allowed to gel at roo temperatures. This generally takes a whole day. The gel is fed through a chopp into ice cans of 100-lb. capacity. These remain in the freezing room at a temper ture of 14°F. for about 2 days. The frozen gel is thawed in tanks at about 50° and then fed into a "dewaterer." This is an ordinary rotary filter, which retai wet agar on the screen and removes by suction the washing water containing solub impurities.

The purified agar flakes, now containing about 90% moisture, are fed into stack dryer where they are agitated by a blast of hot air heated to about 215° until the moisture content is reduced to about 35%. At this stage the partial dried flakes are light enough to be carried over the top of the stack and into the do pipe. The flakes are discharged into a sodium hypochlorite bleaching tank at roo temperature. When the flakes are satisfactorily bleached, sodium sulfite soluti is added to reduce the excess hypochlorite. The bleached agar is thorough washed and finally dehydrated in the stack dryers. This time two dryers are use the first dehydrating the flakes to 35% and the second to less than 20% moisture the amount allowed by the U.S.P. XII.

The dried agar flakes may be sacked for the market or may be further grou for special uses. The grinding is effected by a swing-hammer mill equipped with suction fan and cyclone collector.

Production

The world's annual production of agar is about 6,000,000 lb., about 90% which comes from Japan. Production in the United States fluctuates considera from year to year; the current annual production is about 200,000 lb. Rus produced 121,000 lb. and China about 75,000 lb. in 1936. During World War necessity forced several countries to prepare agar from local seaweeds. Con quently, Mexico, South Africa, Australia, and New Zealand have developed th own agar industries and are now producing sufficient quantities of agar for their o use.

Grades and Specifications

Being made in a few relatively modern factories, American agar is unifor high in quality, and is therefore not graded. Japanese agar, on the other hand primarily a homemade product, and comes from hundreds of small and large f tories, most of which use rather crude and primitive methods. Consequently th is a considerable variation in the quality of Japanese agar. In 1939, the Japan Association of Agar Manufacture was formed, and stipulations for agar inspect and grading were formulated. Agar was graded in accordance with its exter appearance and its quality as judged by the gel strength of the product and by content of crude protein and of hot-water residues.

The U.S.P., XIII, 1947, stipulates that agar contains not more than 1 per cent
oreign organic matter (pp. 710–11), and yields not more than 0.5 per cent of
-insoluble ash and not more than 20 per cent of moisture when dried at 105°C.

For bacteriological agar, the United States Army has its own specifications.
rder to be acceptable, the agar should "have little or no color, odor, or taste";
ould "be clean and free of foreign matter"; it should "possess good water ab-
ing and retentative properties" and should "be practically free of starch and
tral in reaction"; its insoluble matter should not exceed 0.1% by weight; and
% gel of it should have a hard enough surface to "support a weight of 49.33
ns per square cm. for two minutes" (7).

Uses

Agar is a valuable colloidal substance principally because of its strongly hydro-
ic nature and its high gel-strength quality. Generally speaking, it is used
re bulk is wanted, or where a suspending, stabilizing, thickening, or gelling
nt is desired.

Agar serves as an article of food in various Oriental preparations. It is well
wn in China as a substitute for the expensive "bird's nest." Being practically
gestible by man, it is commonly used as roughage, and in certain breakfast foods
special bakery products for laxative purposes. It is extensively employed in
king jellies and the jelly type of desserts, and in preparing confectioneries and
rshmallows. It serves as a thickener in soups, sauces, and gravies, and as a
bilizer in icings, meringues, fillings, and salad dressings. Agar is useful in canning
preserving meat and poultry, and in making sausage casings. It also serves in
bilizing ices and sherbets, in making cream cheese of the Neufchâtel type, and in
paring malted milk and acidophilus milk.

Agar is commonly taken as a mechanical laxative, and is a constituent of
rolatum–agar emulsions. It is employed in making pills, capsules, ointments,
th paste, and various pharmaceutical and cosmetic jellies and creams (see *Cos-
ics*; *Pharmaceuticals*). Agar is the standard material in the preparation of solid
robiological culture media and is indispensable in the routine sanitary analyses of
ter and milk. In addition, agar serves in scientific laboratories as an embedding
dium for microtome sectioning, as a vehicle in the standard *Avena* test for plant
wth hormones, and as a coagulant for barium sulfate precipitation. In the electro-
ting of lead, addition of small amounts of agar renders the disposition of lead most
isfactory. Agar is also used in certain hygrographs for measurement of high
nidity. A system employing a calomel-saturated quinhydrone cell with an agar
l potassium chloride bridge is quick, accurate, and convenient in the measurement
pH of soil samples. In agriculture, agar is useful as an insecticide activator and
rier, and in making coatings for nitrogen bacteria cultures.

Agar is extensively used in prosthetic work (see *Dental supplies*). It is the
sic material in most dental impression materials. In highly critical work, such as
ays and fixed bridges, agar-based compounds are almost the only materials em-
yed. Agar is an excellent suspending agent in wiredrawing lubricants, especially
tungsten wires for making electric bulbs. It is used in clarifying liquors such as
e and schnapps, in sizing paper and textiles, in the manufacture of submarine
rage batteries, and in making backings for films and gelatinous rolls for hecto-
phs.

Before World War II, the United States used about 650,000 lb. of agar annually Of this, about 100,000 lb. went to each of the following: laxatives, microbiologica culture media, the bakery industry and the confectionery industry; 75,000 lb. t dental impression materials; 50,000 lb. to meat packing and to emulsifiers; 25,000 lb to cosmetics; and 50,000 lb. to miscellaneous uses.

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(11) U.S. Pat. 1,726,942 (Sept. 3, 1929), John Becker (to American Agar Co.).

C. K. Tsen

Contribution No. 351

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ALGIN

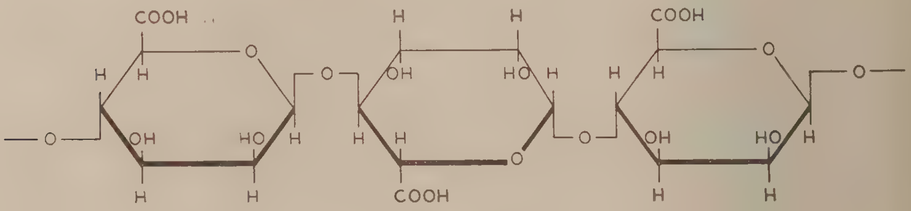
Algin is a seaweed colloid (phycocolloid) extracted by alkalies from brown algae (Phaeophyta), especially members of the kelp order (Laminariales) (see *Seaweed colloids*). It probably occurs as a mixture of alginic acid and certain salts. Algin is sold generally as a white powder, and sometimes in the form of a paste. The latter is a crudely prepared algin product which contains cellulose and other impurities from the kelp. Purified algin may be marketed as pure sodium alginate or as a mixture of sodium alginate and other substances. American algin is known under several trade names, the best known of which is Dariloid, which is a mixture of sodium alginate and other substances, such as dextrin, sucrose, and a phosphate. English algin is marketed under the trade name of Manucol, a few grades of which are differentiated. Various brands of algin on the market differ from each other in their viscosity and in the foreign substances they contain. Besides sodium alginate, another soluble alginate, ammonium alginate, and an insoluble one, calcium alginate, are also available on the market.

In 1883, the English chemist, E. C. C. Stanford, reported that by digesting *Laminaria* fronds with sodium carbonate, a glutinous mass was obtained, which, when evaporated to dryness, presented "an appearance which is not unlike gum tragacanth." To this new substance, its discoverer gave the name "algin," derived from the word alga. This term was originally proposed to designate the substance *in situ* in the plant. Since it is not definitely known what this particular substance actually is in the natural condition, the term has come to be loosely used. As employed by its discoverer and later authors, it has been applied additionally to: (*1*) alginic acid, (*2*) sodium alginate, (*3*) soluble alginates, and (*4*) the alginic compounds in general. Since the principal alginic compound now being manufactured and put on the market is sodium alginate rather than the unstable alginic acid, the term algin has frequently been used interchangeably with sodium alginate.

Stanford believed his alginic acid to be a nitrogenous compound, and even proposed the following formula for it: $C_{76}H_{76}O_{22}(NH_2)_2$. Krefting (1896) by improved methods showed that the alkali extract of seaweed, presumably kelp, was nonnitrogenous and called it "tang acid" to differentiate it from the impure alginic acid of Stanford. Later authors, however, prefer to retain the terms "algin" and "alginic acid" as proposed by Stanford, in spite of the fact that his product was contaminated.

Chemical Nature

Alginic acid is a polyuronic acid composed entirely of mannuronic anhydride residues, in which the hydroxyl groups are attached to carbon atoms 2 and 3, while bridge and ring are attached to carbon atoms 4 and 5. Although evidence is not yet sufficient to decide between pyranose and furanose structures, the former is believed to be more probable, in view of the large negative rotation of alginic acid and its resistance towards hydrolysis. Thus, the mannuronic acid units are linked in such a way that the carboxyl group on each unit is free to react while the aldehyde group is shielded by linkage. The following formula represents the arrangement of the mannuronic residues in alginic acid according to Hirst, Jones, and Jones (1939):



Alginic acid

Like agar, algin is believed to occur in nature as a cell wall constituent, and probably exists as a mixture of the acid itself and its calcium, magnesium, and alkali metal salts in various proportions which show interspecific and seasonal differences.

Properties and Reactions

Alginic acid is insoluble in cold, and only slightly soluble in boiling water. When moist, it is capable of absorbing several times its weight of water. When dried, it becomes very hard, horny, and resistant to solvents. It is insoluble in alcohol, ether, and glycerol. It does not reduce Fehling solution, but rapidly forms reducing substances if dried at 100°C. or if boiled with dilute acid. Its optical activity is high, with rotation values varying from —132.6° to —169.2°, according to different workers. It has weak acid properties, but is sufficiently acidic to liberate carbon dioxide from carbonate solutions. It has a theoretical neutralization equivalent of 176.

Alkali metal salts of alginic acid, as well as the ammonium, magnesium, and lower-amine salts, are water-soluble. Other alginates are insoluble in water. The soluble alginates are strongly hydrophilic colloids, yielding highly viscous solutions at low concentrations. A 1% sodium alginate solution, for instance, may have a viscosity of about 1000 centipoises at 17°C. The viscosity of algin solutions, however, varies considerably with the manufacturing methods.

The pH of sodium alginate resulting from the stoichiometrical combination of alginic acid and sodium hydroxide is approximately 7.7. In industry, it is practical to employ algin with a pH range of about 4 to 10. Below pH 4 the alginic acid tends to precipitate, while above 10 the algin loses viscosity rapidly and tends to become unstable. Increases in temperature reduce the viscosity of algin solutions but do not cause any significant depolymerization below 50°C.

Sources and Production

The United States and England are the principal algin-producing countries, although Norway, France, Russia, and Japan have produced some. On the Pacific coast of North America, *Macrocystis pyrifera*, the well-known giant kelp of California, is the sole raw material employed in the industry, although there are several other large kelps which also have high algin contents. *Macrocystis* grows on submarine rocks twenty-five to ninety feet deep and sends up its leafy fronds, which float on the surface. Where environmental conditions are favorable, as in southern California, it forms extensive beds from a few hundred yards to two or three miles wide and several miles long. Consequently, it is possible to harvest the kelp by means of a specially adapted motor-run barge, which cuts the seaweed with a horizontal cutting blade at a depth of about four feet, and an endless chain elevator, which hoists the kelp on board. A modern kelp harvester can cut as much as three hundred tons per day. The enormous kelp resources of California and the mechanization of the harvesting process make possible the present successful algin industry on the west coast.

On both sides of the Atlantic, algin is extracted from species of *Laminaria*, especially *L. digitata* (horsetail kelp) and *L. saccharina* (broadleaf kelp). These grow abundantly on submarine rocks ten to fifty or more feet deep. In North America, commercial quantities of these kelps are located in Maine and Nova Scotia. They are mostly harvested with a grapple hauled at a depth of twelve to fifteen feet from a power boat, and to a lesser extent by hand dragging or sickling from a dory. In the British Isles, these kelps are known as deep-sea tangles and are frequently washed up on the shore in large quantities, where they are collected. In Normandy, the kelps are cut by means of sickle-shaped knives fastened on long poles and operated from small boats. Norway is another important kelp-producing country. Before World War II, the United States imported large quantities of kelps from Europe for the manufacture of algin.

There are no published statistical data on the production of algin. The United States probably produces annually more than two million pounds, the majority of which comes from the west coast. The annual algin output in England and other countries is not known.

Manufacture

PRINCIPLE OF MANUFACTURE

Commercial preparation of algin is based on the principle that the natural "algin" in the kelp, probably a combination of calcium alginate and alginic acid, is insoluble in water, but is easily converted by soda solution into the water-soluble sodium salt. Kelp is therefore digested with sodium carbonate or hydroxide solution, the resulting viscous liquor separated from the residue, and alginic acid subsequently precipitated by the addition of a strong mineral acid. To facilitate purification and bleaching of the product, some manufacturers adopt an intermediate procedure involving precipitation of calcium alginate prior to the acid precipitation. Since alginic acid is rather unstable, sodium alginate is generally the product manufactured. By simply dissolving the acid in sodium carbonate solution, sodium alginate is obtained. Other salts, such as ammonium alginate and calcium alginate, are also prepared commercially.

EARLY PROCESSES

In Stanford's original "wet" process, algin was prepared as a by-product in the manufacture of iodine and potash to enable the Scottish iodine factories to utilize kelp as their raw material in competition with the South American iodine industry. After a cold-water treatment, the *Laminaria* is digested for 24 hours with one-tenth its weight of sodium carbonate. The resulting viscous mass is filtered through coarse linen filter bags. Sulfuric or hydrochloric acid is added and alginic acid precipitates in light-gray, gelatinous flocks. The acid is washed, pressed, and dried, and constitutes the primary product of Stanford's process. The product may be sold in this condition, or as a sodium, potassium, or ammonium salt made by dissolving the acid in the respective carbonate solution.

During World War I, algin was made by Hercules Powder Company as a by-product of the fermentation process in the manufacture of potash and calcium acetate and its solvent derivatives. The giant kelp of California, *Macrocystis pyrifera*, served as the raw material. It was fermented in large tanks. After fermentation the resulting liquor was separated from the residue and potash, calcium acetate, and other organic salts were made from it. The unfermented kelp residue, screened from the fermentation vats, was used for the preparation of algin by a process similar to that of Stanford.

GREEN'S "COLD" PROCESS

Stanford's original process for algin manufacture has undergone a series of improvements by several investigators in various countries. In the United States there are at present two basic patented processes. One of these may be represented by Green's "cold" process of the Pacific coast and the other by the Le Gloahec-Herter process of the Atlantic coast. Green's "cold" process (8) (see Fig. 1) is characterized by being largely conducted at the relatively low temperature of 50°F.

1. Leaching. Freshly harvested kelp is introduced into a leaching tank with cold water previously acidulated to 0.33% hydrochloric acid. The leaching is continued until the salt content of the kelp is reduced from its original 35–40% to 5–15%. This requires from a few hours to a day. The leach water is drained off and discarded.

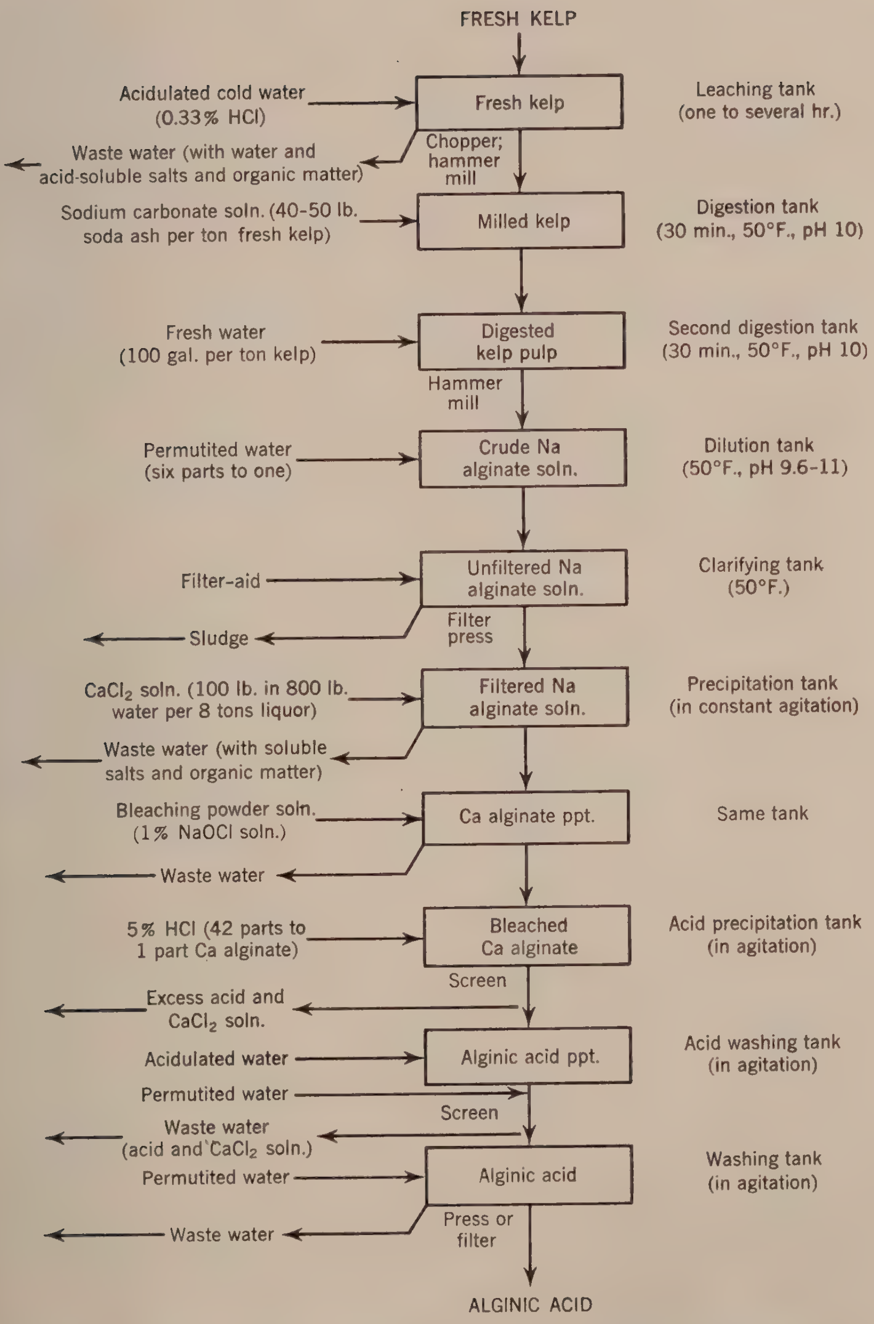

FRESH KELP
Acidulated cold water (0.33% HCl)
Fresh kelp
Leaching tank (one to several hr.)
Waste water (with water and acid-soluble salts and organic matter)
Chopper; hammer mill
Sodium carbonate soln. (40-50 lb. soda ash per ton fresh kelp)
Milled kelp
Digestion tank (30 min., 50°F., pH 10)
Fresh water (100 gal. per ton kelp)
Digested kelp pulp
Second digestion tank (30 min., 50°F., pH 10)
Hammer mill
Permutited water (six parts to one)
Crude Na alginate soln.
Dilution tank (50°F., pH 9.6-11)
Filter-aid
Unfiltered Na alginate soln.
Clarifying tank (50°F.)
Sludge
Filter press
CaCl₂ soln. (100 lb. in 800 lb. water per 8 tons liquor)
Filtered Na alginate soln.
Precipitation tank (in constant agitation)
Waste water (with soluble salts and organic matter)
Bleaching powder soln. (1% NaOCl soln.)
Ca alginate ppt.
Same tank
Waste water
5% HCl (42 parts to 1 part Ca alginate)
Bleached Ca alginate
Acid precipitation tank (in agitation)
Screen
Excess acid and CaCl₂ soln.
Acidulated water
Alginic acid ppt.
Acid washing tank (in agitation)
Permutited water
Screen
Waste water (acid and CaCl₂ soln.)
Permutited water
Alginic acid
Washing tank (in agitation)
Waste water
Press or filter
ALGINIC ACID

Fig. 1. Green's cold process of algin manufacture—plant flow sheet diagram (5).

2. Digestion. Leached kelp is chopped into convenient sizes, and fed to a hammer mill shredder equipped with a 1/8-inch mesh screen. It is then placed in a soda digestion tank. Sodium carbonate is added in the ratio of 40 to 50 lb. to each ton of freshly harvested kelp. With pH maintained at 10, the digestion is usually completed in 30 minutes. The mixture may be left for as long as 24 hours without any adverse effect on the product. The resulting pulp is passed through another hammer mill equipped with a 30-mesh screen, and 6 volumes of water, softened by the Permutit process, are added. The pH is about 9.6 to 11. The dilution is merely to facilitate filtration.

3. Clarification. Crude sodium alginate (containing cellulose and other impurities), either dried or as a paste, is satisfactory for certain purposes, for instance, in boiler-water treatment. Most industries, however, require a highly purified product free from contaminants. To purify the product, the crude liquor is pumped into a clarification tank, and to it is added filter-aid, such as diatomaceous earth. The mixture is then pumped through a mechanical filter press. At this stage, the temperature may be temporarily raised to about 120°F. to facilitate the filtration. Other methods of clarification may be used, such as centrifuging, vacuum filtration, sand bed filtration, or mere gravitational settling of the cellulose material.

4. Calcium Alginate Precipitation and Bleaching. The filtered liquor is slowly added to a 10% calcium chloride solution under constant agitation. Calcium chloride is used in the proportion of about 100 lb. of the salt to 8 tons of the algin liquor. Calcium alginate is precipitated, and when agitation is stopped, gradually rises to the top. The remaining liquor containing water-soluble salts and organic matter is drained off. More water is added to the calcium alginate in the same tank into which is introduced a suitable bleaching agent, such as sodium hypochlorite. The amount of hypochlorite to be added depends on the color of the crude product. The "cold" process produces a whiter crude product than the other processes and generally about 1% hypochlorite is sufficient. Excessive bleaching will have an adverse effect on the quality of the final product.

5. Acid Precipitation. Separated from the surplus water, the bleached calcium alginate precipitate is introduced into a 5% hydrochloric acid solution in the ratio of 1 to 42. Fibrous alginic acid is formed and is passed through a screen to remove the remaining hydrochloric acid and the calcium chloride resulting from the chemical reaction. The drained alginic acid precipitate is introduced into a second tank of acidulated water, agitated, and pumped over another screen. This treatment is repeated until the precipitate is washed free of calcium salts. Enough water is used in the washing to raise the pH of the acid above 1.9 and simultaneously to reduce the calcium content of the product.

Purified alginic acid is concentrated by means of a press or filter and temporarily stored in a refrigerated room, or converted into the sodium or other salts by treating with the corresponding carbonate, oxide, or hydroxide. The alginate thus formed is dried by one of the standard methods, ground, screened, and packaged or mixed with other ingredients to form one of the several commercial products.

LE GLOAHEC-HERTER PROCESS

This process (9) (see Fig. 2) takes advantage of the following facts: (*1*) Dilute solutions of alkaline earth salts such as calcium chloride will dissolve and conse-

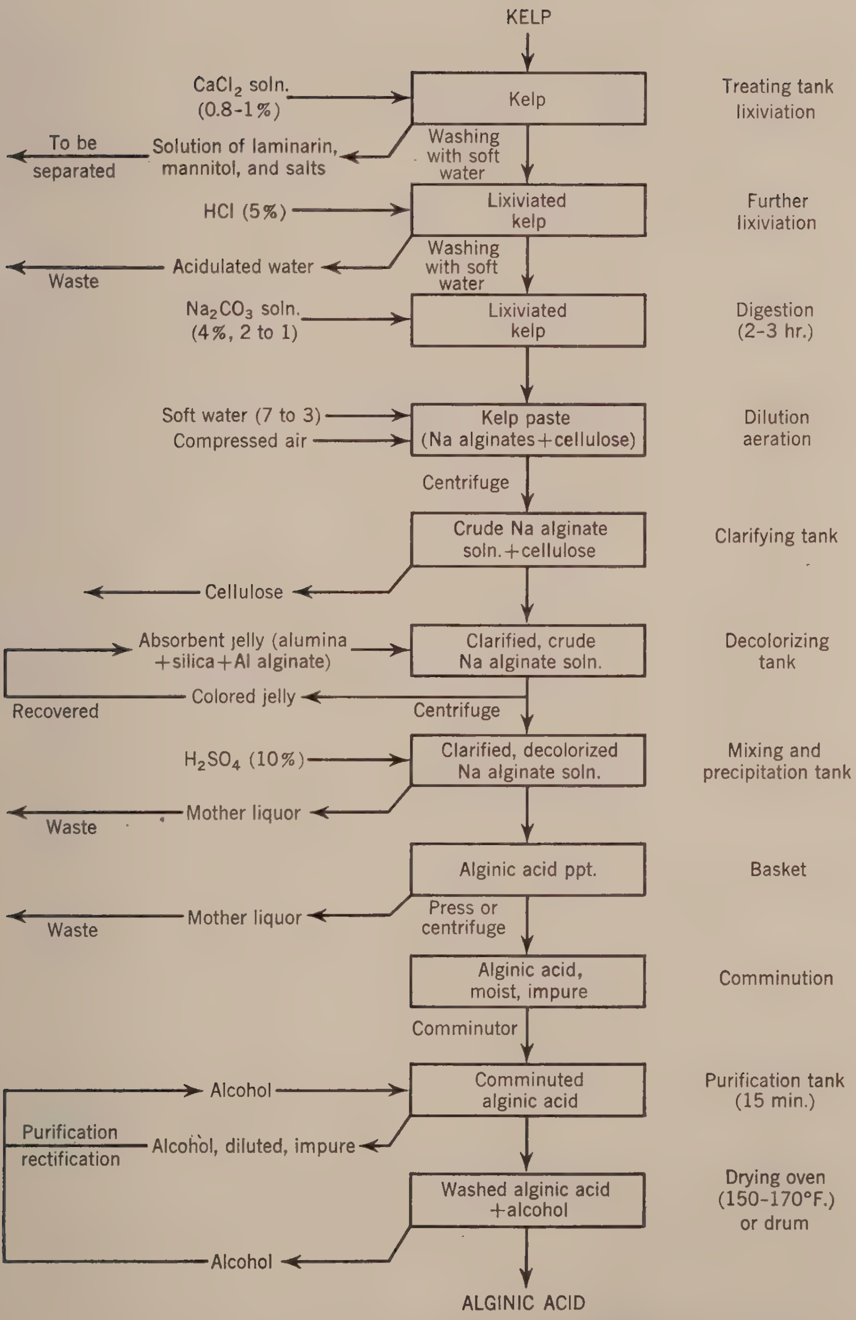

KELP
CaCl$_2$ soln. (0.8-1%)
Kelp
Treating tank lixiviation
To be separated
Solution of laminarin, mannitol, and salts
Washing with soft water
HCl (5%)
Lixiviated kelp
Further lixiviation
Waste
Acidulated water
Washing with soft water
Na$_2$CO$_3$ soln. (4%, 2 to 1)
Lixiviated kelp
Digestion (2-3 hr.)
Soft water (7 to 3)
Compressed air
Kelp paste (Na alginates+cellulose)
Dilution aeration
Centrifuge
Crude Na alginate soln.+cellulose
Clarifying tank
Cellulose
Absorbent jelly (alumina +silica+Al alginate)
Clarified, crude Na alginate soln.
Decolorizing tank
Recovered
Colored jelly
Centrifuge
H$_2$SO$_4$ (10%)
Clarified, decolorized Na alginate soln.
Mixing and precipitation tank
Waste
Mother liquor
Alginic acid ppt.
Basket
Waste
Mother liquor
Press or centrifuge
Alginic acid, moist, impure
Comminution
Comminutor
Alcohol
Comminuted alginic acid
Purification tank (15 min.)
Purification rectification
Alcohol, diluted, impure
Washed alginic acid +alcohol
Drying oven (150-170°F.) or drum
Alcohol
ALGINIC ACID

Fig. 2. Le Gloahec-Herter process of algin manufacture—plant flow sheet diagram (5)

quently remove laminarin and mannitol from the kelp without any harmful effect on the algin. The kelp may subsequently be demineralized by washing in soft water. (*2*) Clarification of the liquor may be effected by charging the solution with gaseous bubbles, which, when ascending to the surface, carry with them the cellulose together with adherent impurities. Thus, filtration with the help of a filter-aid and through a filter press is not necessary. (*3*) Decolorization of the product may be effected by a pigment-adsorbing jelly or a protein coagulant. The usual step of calcium alginate precipitation, which primarily serves to facilitate bleaching and purification, may thus be omitted.

1. Lixiviation. Kelp used in this process may be freshly harvested or air-dried. To 1 volume of the dried kelp, 3 volumes of 0.8–1.0% calcium chloride solution are added. Lixiviation may be carried out hot or cold, preferably the latter. This removes the majority of the laminarin and mannitol in the kelp, which is subsequently washed with soft water to remove the calcium chloride as well as the remaining laminarin, mannitol, and various salts. Washing is stopped when the wash water contains only about 0.5% solids. The washed kelp may be further subjected to an additional treatment with 5% hydrochloric acid to dissolve any residual alkaline earth salt. It is washed again with soft water.

2. Digestion. Two volumes of 4% sodium carbonate solution are added to each volume of the well-lixiviated kelp. This may be performed in any suitable vessel. Mixing is facilitated by beaters such as those commonly used in pulp making. Maceration is continued until the cellulose is reduced to fine particles and a homogeneous paste obtained. Digestion requires about 2 hours at 104°F. and about 3 hours at room temperature.

3. Clarification. To 3 volumes of the kelp paste 7 volumes of water are added. The mixture is beaten to a homogeneous suspension and air introduced through fine apertures to stir up the entire mass vigorously. Oxygen in the air is said to aid in making a product of high viscosity. If oxygenating agents such as ozone or hydrogen peroxide are employed, agitation is effected mechanically. The oxygenated liquor is then passed continuously at high speed through a centrifuge, which charges it with air bubbles. The resulting emulsion is conveyed to a clarification tank. Upon standing for 6 to 10 hours, the cellulose particles agglomerate to form a rather compact cake floating on the liquor. The clarified liquor can now be removed without difficulty.

4. Decolorization. The clarified liquor, still colored by seaweed pigments, must be decolorized to yield a superior product. An adsorbent jelly made of hydrated alumina, gelatinous silica, and aluminum alginate is preferred, although others of similar nature may be used. The jelly is added to the colored liquor in about 20–25% of the weight of the dry alginous material. After some stirring, the pigments adhere to the jelly, which is then removed by centrifuging. Reclamation of the jelly is effected by washing with alcohol or other organic solvents, which may be recovered by standard methods.

5. Acid Precipitation. To the clarified and decolorized liquor a strong mineral acid such as hydrochloric acid is added, and the pH maintained at 2.8 to 3.2. The acid and the alginous liquor are introduced separately into a mixing baffle, slightly inclined inside a tank. Alginic acid precipitates and flows at once to the adjoining tank. This minimizes contact of the precipitate with the mineral acid, which otherwise tends to have an adverse effect on the final product. Carbon dioxide evolved from the reaction between sodium carbonate and hydrochloric acid helps to keep the precipitate afloat, thus facilitating its overflow into the next tank.

6. *Purification.* Alginic acid, thus precipitated, is placed in baskets and allowed to drain. Freed from the remaining liquor by pressing or centrifuging, the precipitate is comminuted and further purified by washing with solvents such as ethyl alcohol in a vessel provided with a filter plate. Alternate methods of purification include ordinary dialysis and electrodialysis.

7. *Dehydration.* The purified alginic acid still contains some adherent alcohol and is dried in a specially constructed oven at 150–170°F. A method of purifying and drying the alginic acid in special rotating drums has been suggested. In both cases, the alcohol may be employed once more or reclaimed. Finally, the alginic acid is converted into its sodium or other salts by the regular methods.

8. *Later Improvements.* An improvement of the process (10) consists in decolorizing the alginous material by a preliminary treatment with formaldehyde, tannic acid, or other protein coagulants. The protein in the kelp, when coagulated by such chemicals, adheres to the cellulose, and to this coagulated protein–cellulose complex, chlorophyll and other plant pigments will eventually be affixed. These pigments may later be recovered if so desired.

Kelp is demineralized as usual and soaked for an hour in 2.5 tons of a formaldehyde solution containing 22 lb. of the chemical. Thus treated, the kelp is taken out and stored for 15 to 21 days, during which period there is a substantial fixation of the colored matter on the protein–cellulose mixture. When sodium carbonate solution is later added to the treated kelp, it dissolves only the alginous matter, leaving the cellulose–protein–pigments complex intact. The resulting sodium alginate solution can thus be easily separated from the impurities. The process from this point is the same as already described above, except the decolorization by alumina–silica–alginate jelly is no longer necessary.

9. *Recovery of Laminarin and Iodine.* The leach water from the Le Gloahec-Herter process contains a considerable amount of laminarin and iodine. Methods are patented (11,12) for the recovery of these substances.

Uses

Like agar and other seaweed colloids, algin is a valuable substance wherever a hydrophilic colloid possessing marked gelling, suspending, emulsifying, thickening, and water-holding properties is required. Unlike agar, it is chemically active, reacting with various metallic salts and acids. Consequently, in certain respects its uses are limited, while in others it serves especially well because of its reactivity. For example, many of the present industrial uses of algin are based on the fact that the addition of a calcium salt to an algin solution produces an immediate precipitate of gelatinous calcium alginate. Thus, by the controlled release of calcium ions, through the use of a relatively insoluble calcium salt, such as calcium citrate, the solutions may either be thickened or converted into rigid gels in accordance with the amount of the calcium salt added. The rate of the setting of the gel may also be controlled by the introduction of salts, such as a soluble phosphate, which form calcium salts more insoluble in water than calcium alginate.

In the preparation of algin solutions for use in food and other industries, water warmed to about 140°F. and high-speed stirring are required in order to effect quick solution. Algin solutions are readily decomposed by bacterial action if allowed to stand for prolonged periods. Hence, preservatives are often needed for algin preparations.

The most important use of algin is undoubtedly in stabilizing ice creams (see *Ice cream*). In making ice creams, a colloid is needed to impart smooth body and texture to the frozen product and to prevent coarsening due to the formation of large ice crystals during storage. It should not in any way mask the flavor of the product. Algin is found to be ideally suitable for these purposes, and is used as an ice cream stabilizer probably more than any others, including the once-standard substance, gelatin. It has been estimated that in the United States, the largest ice-cream-consuming country in the world, more than 50% of the factory-made ice cream is stabilized with algin. This kelp colloid is also extensively used in stabilizing ices. In chocolate milk it serves as a suspending agent for the cacao particles and in milk puddings as a gelling agent. Its numerous uses in food industries include the preparation of jellies, jams, icings, meringues, fillings, cheese, whipping creams, milk powders, oleomargarines, candies, fruit juice powder, sausage casings, and cakes.

Algin serves as a base for various pharmaceutical preparations and as a constituent in pills and tablets (see *Pharmaceuticals*). A hemostatic agent has been derived from it for use in gauzelike form absorbable by tissue fluids. Algin has also been used as a component of sulfanilamide and similar ointments. In the cosmetic industry, it is an excellent vehicle for hand lotions of the saponified type, and is a valuable base for various cosmetic jellies, creams, and tooth pastes (see *Cosmetics*). To some extent, it has replaced tragacanth and other natural gums in the preparation of greaseless lubricating jellies.

One of the important industrial uses of the alginic compounds is as a latex creaming agent in the manufacture of natural rubber (see *Rubber compounding and manufacture*). Ammonium alginate is an excellent substance for this purpose, and may possibly be the best. It is said to be used similarly in processing synthetic rubber. Both ammonium and sodium alginates are widely used as suspending and emulsifying agents in the manufacture of casein emulsion paints. Sodium alginate is useful in the treatment of boiler water for preventing incrustation. It reacts with the calcium salts present in the water and forms globular flocculent precipitates. These envelop other sediment to give a soft, pasty sludge in the boiler and can be easily blown out at regular intervals.

In dentistry algin serves as a dental impression material (see *Dental supplies*). Although algin-based preparations do not produce as accurate molds as do the agar-based ones, they are somewhat more convenient to employ and are therefore extensively used by dentists for general work. Algin is also used to cover and protect dentures made of acrylic resin. In relative ease of uniform application, it has an advantage over tin foil, the material traditionally used for this purpose.

Algin is a useful sizing material and is superior to starch in that it fills the cloth more completely, is tougher, and is more elastic (see *Textile finishing*). As soon as algin has impregnated the cloth, it can readily be made insoluble by treatment with dilute acids, lime water, or metallic salts, and thus a waterproof cloth is obtained. Ammoniated aluminum alginate can also be used in the preparation of waterproof fabrics since it becomes insoluble after drying. Algin is extensively used as a thickener in printing pastes. Triethanolamine alginate is employed as a coating material for solid surfaces. In recent years, great development has been made on the use of algin in the manufacture of textile fibers. Specially treated algin fibers have already found application because they are alkali-resistant and fireproof. Chromium alginate fibers have been used in making camouflage nettings.

Incorporated in insecticide sprays, algin activates the effective chemical and so greatly reduces the amount required. In certain fire-retarding compounds, aqueous sodium or ammonium alginate solution is used to suspend the finely ground fire-retarding chemicals, such as monoammonium phosphate. Algin is also employed in the purification of beet juices in sugar manufacture, in oil well drilling muds to seal off porous formations, as a medium for separating plates in the manufacture of storage batteries, as a binder for printer's ink, as a binder to make a seaweed charcoal product for heat insulation of boilers, in the dressing of mildew-resistant canvas and burlap, as a binder in cartridge primers, in finishing leathers, and in the preparation of a color-absorbing material.

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C. K. Tseng

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UNIVERSITY OF CALIFORNIA
LA JOLLA, CALIFORNIA

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